POPULATION STRUCTURE AND BEHAVIOR OF PACIFIC HALIBUT

A

THESIS

Presented to the Faculty

of the University of Alaska Fairbanks

in Partial Fulfillment of the Requirements

for the Degree of

DOCTOR OF PHILOSOPHY

By

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Fairbanks, Alaska

December 2006

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Abstract

Pacific halibut (*Hippoglossus stenolepis*) is not managed on regional scales with separate population dynamics, but rather as a single, fully mixed population extending from California through the Bering Sea. However, some of the evidence from which this paradigm was established is questionable and I hypothesize that there are separate spawning populations of Pacific halibut in three regions, the Gulf of Alaska, Bering Sea and Aleutian Islands, because these regions are geographically separated by land masses and/or deep water passes that may prevent movement by adults. Pop-up Archival Transmitting (PAT) tags were attached to Pacific halibut in each region to examine their movement and behavior. First, geolocation by ambient light was able to discern basin-scale movements of demersal fishes in high latitudes and therefore this technique provided a feasible method for providing scientific inference on large-scale population structure in Pacific halibut. Second, because seasonally low ambient light levels and inhabitation of deep water (>200 m) restricted geolocation by light during winter, an alternative method, a minimum distance dispersal model, was developed for identifying migration pathways of demersal fish in the Gulf of Alaska based on daily maximum depth. Third, the PAT tags provided no evidence that Pacific halibut in the southeastern Bering Sea and Aleutian Islands moved among regions during the mid-winter spawning season, supporting my hypothesis of separate populations. Fourth, geographic landforms and discontinuities in the continental shelf appeared to limit the interchange of Pacific halibut among areas and possibly delineate the boundaries of potential populations in the Gulf of Alaska and eastern Bering Sea, with apparent smaller, localized populations

along the Aleutian Islands. This possible population structure may be reinforced by regional behavioral variation in response to the environment. Future research should be directed at quantifying the exchange of individual fish among regions for possible local area management plans that more accurately reflect population structure.

Table of Contents

List of Figures

Page

List of Tables

Page

List of Appendices

Page

Acknowledgements

I would like to thank each of my committee members for their advice and input into my research: Dr. Brenda Norcross, my major advisor at University of Alaska Fairbanks (UAF), guided my research, provided invaluable assistance in manuscript preparation and exposed me to the field of fisheries oceanography through her courses at UAF and encouraging me to attend professional meetings; Dr. Jennifer Nielsen of the United States Geological Survey–Alaska Science Center (USGS–ASC) conceived of the idea of satellite tagging Pacific halibut and generously supported my graduate career; Dr. Timothy Loher of the International Pacific Halibut Commission (IPHC) provided invaluable logistical support for my project, acted as my liaison at the Commission, and was always available for lengthy discussions on Pacific halibut biology and ecology; Dr. Nicholas Hughes of the School of Fisheries and Ocean Sciences (SFOS) at UAF deepened my understanding of fish ecology; and Dr. Tom Weingartner of the School of Fisheries and Ocean Sciences at UAF was a vast source of knowledge regarding physical oceanography and helped make the link between "fisheries" and "oceanography."

This project was made logistically possible by the help of friends, co-workers at USGS–ASC, fishing captains, International Pacific Halibut Commission (IPHC) Sea and Port Samplers, and the IPHC Annual Setline Survey Managers, all of who are acknowledged individually in each chapter. A special thanks goes to Dr. Bruce Leaman, Executive Director of the IPHC, for his continued support of the satellite tagging project of Pacific halibut.

Finally, I want to thank Susan Seitz, my wife, best friend and skijorer extraordinaire. She deserves some type of award for her patience, tolerance and steadiness.

Partial funding for this project was provided by the Exxon Valdez Oil Spill Trustee Council, the International Pacific Halibut Commission, the U.S. Geological Survey–Alaska Science Center and the University of Alaska Fairbanks School of Fisheries and Ocean Sciences. The findings presented by the authors are their own and not necessarily the position of the EVOS Trustee Council.

CHAPTER ONE

Introduction

Pacific halibut *Hippoglossus stenolepis* inhabit continental shelf areas of the eastern Pacific Ocean from California to the Bering Sea. Because of their large size (up to 250 kg) and fine flesh quality, Pacific halibut have experienced sustained commercial exploitation for the last century (International Pacific Halibut Commission, 1998). Currently, this species supports one of the most-profitable fisheries in the Gulf of Alaska and eastern Bering Sea with annual coast-wide landings averaging approximately 70 million pounds over the last five years (ex-vessel value of ~US$170 million; International Pacific Halibut Commission, unpublished).

Generally, adult Pacific halibut throughout their range feed during the summer on the continental shelf, migrate in late fall to the continental slope to spawn during the winter, and in early spring migrate back to the same summer feeding grounds each year (Skud, 1977). The spawning season occurs from early November to late March on grounds concentrated on the continental slope (St-Pierre, 1984). Winter surveys have confirmed active spawning at depths from 180 to 450 m (International Pacific Halibut Commission, 1998), while emerging data from electronic tags suggest that spawning likely occurs to depths of 800 m (Seitz et al., 2003; Loher and Seitz, 2006; Chapter Four). In addition to the continental slope, it is believed that spawning also occurs in depressions on the continental shelf (St-Pierre, 1984).

Currently, the International Pacific Halibut Commission (IPHC) does not manage Pacific halibut on a regional scale with separate population dynamics, but rather as part of a single, mixed population in the entire eastern Pacific Ocean including the United States and Canada. This management paradigm was largely established due to four lines of evidence: (1) conventional tagging experiments (Skud 1977, Kaimmer 2000), (2) genetic studies (Tsuyuki et al. 1969, Grant et al. 1984, Bentzen et al. 1999), (3) spawning ground surveys (St-Pierre 1984), and (4) a review of larval surveys (St-Pierre 1989).

Recently, it is recognized that several marine fish species have a more complex population structure than previously realized, and in many cases, management units contain population complexes with several spawning components (Stephenson 1999). This may be the case with Pacific halibut; some of the evidence from which the single population paradigm was established is questionable (Chapter Four).

I hypothesize that there are separate spawning populations of Pacific halibut in the Gulf of Alaska, Bering Sea and Aleutian Islands because these areas are geographically separated by land masses and/or deep water passes that may prevent movement by adults (Chapter Five). Additionally, each of these three regions has a potential retention area for eggs and larvae (Stabeno et al. 1999). The combination of the barrier to adult movement and the possible retention gyres for eggs and larvae could limit the amount of exchange among regions.

Emerging technologies, such as Pop-up Archival Transmitting (PAT) tags, are able to overcome several limitations associated with traditional methods of investigating population structure. From October 2000 to March 2002, a pilot study in which PAT tags

were attached to Pacific halibut was conducted to assess the feasibility of using these tags as a tool for identifying critical habitat of demersal fishes in high latitudes (Seitz et al., 2002, 2003). This technology successfully allowed us to gain new insights into Pacific halibut behavior and ecology, such as determining winter locations of PAT-tagged fish, inferring migration timing and depth of seasonal migrations, and determining environmental conditions experienced by Pacific halibut. In the pilot study, we did not evaluate one of the major features of PAT tags: geolocation by light.

The first part of the present study examined the scale and effectiveness of ambient light geolocation estimation for demersal fishes, including Pacific halibut, in high latitudes (Chapter Two). Because seasonally low ambient light levels and inhabitation of deep water (>200 m) restricted geolocation by light during winter, I developed an alternative method of identifying locations and migration pathways of demersal fish in the Gulf of Alaska based on daily maximum depth (Chapter Three).

Following the pilot study, the study area was expanded and additional adult Pacific halibut were PAT tagged in the Bering Sea and Aleutian Islands. The goal of this study was to investigate whether Pacific halibut that feed during the summer in the Bering Sea and Aleutian Islands disperse to winter spawning grounds in the Gulf of Alaska (Chapter Four). These results were integrated with PAT tagging results from the Gulf of Alaska (Seitz et al. 2003; Loher and Seitz 2006) and I propose a conceptual life history model that describes mechanisms of potential population structure for Pacific halibut (Chapter Five). To conclude, I offer suggestions for future PAT tag research and

recommend several alternative approaches for future research that would fill in life history information gaps of Pacific halibut (Chapter Six).

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CHAPTER TWO

Evaluating light-based geolocation for estimating movement of demersal fishes in high latitudes[1]

Abstract

I evaluated light-based geolocation estimates from pop-up satellite tags in high latitudes because some of the largest fisheries in the world are in areas where this technique has not been assessed. Daily longitude and latitude were estimated using two Wildlife Computers' geolocation software types: 1) Argos Message Processor (AMP) using summary data sent to satellites, and 2) Time Series Processor (TSP) using more detailed data obtained from retrieved tags. Three experiments were conducted in the northern Gulf of Alaska using tags placed on: 1) Pacific halibut in outdoor aquaria, 2) a fixed mooring line at various depths and 3) wild Pacific halibut. TSP performed better than AMP because the percentage of days with geolocation estimates was greater while mean error magnitude and bias were smaller for TSP. Error magnitude increased with depth for both programs, with latitude errors much greater than longitude errors at all depths. Geolocation by light was able to discern basin-scale movements and show that the Pacific halibut in this study remained within the Gulf of Alaska. We conclude that this technique provides a feasible method for providing scientific inference on large-scale population structure in demersal fishes in high latitudes.

[1] Seitz, A. C., B. L. Norcross, D. Wilson, and J. L. Nielsen. In press. Evaluating light-based geolocation for estimating movement of demersal fishes in high latitudes. Fishery Bulletin.

Introduction

Demersal fishes at high latitudes support some of the most lucrative fisheries in the world. An example is the Pacific halibut (*Hippoglossus stenolepis*) fishery off Canada and the United States. Currently, the International Pacific Halibut Commission (IPHC) manages the Pacific halibut population as a single, panmictic stock from northern California through the eastern Bering Sea based on genetic (Grant et al., 1984; Bentzen et al., 1998) and tagging data (Skud, 1977). However, Pacific halibut movements and population structure are not fully understood and mixing may be more restricted than assumed, as evidenced by a number of local depletions in recent years (Hare[2]). A method to estimate movements over large distances is needed to improve the ability to identify populations and manage the harvest. Population structure and movement information is needed for management of several other high latitude fisheries including Atlantic halibut (*Hippoglossus hippoglossus*), Pacific cod (*Gadus macrocephalus*) and Greenland turbot (*Reinhardtius hippoglossoides*) (Godø and Haug, 1988; Shimada and Kimura, 1994; Albert, 2002).

New methods using information collected by electronic tags, which contain miniaturized onboard computers, are providing location estimates of demersal marine fishes (see review in Arnold and Dewar, 2001). One such method, the tidal location method, has been used to geolocate North Sea plaice (*Pleuronectes platessa*) (Hunter et

[2] Hare, S. R. 2005. Investigation of the role of fishing in the Area 4C CPUE decline. Int. Pac. Halibut Comm. Report of Assessment and Research Activities 2004: 185–198. Int. Pac. Halibut. Comm, PO Box 95009, Seattle, WA 98145-2009.

al., 2003). This method compares the tidal range and time of high water, as measured by the depth sensor of the electronic tag, to those predicted by tide models. Unfortunately, we are unable to use this method near Alaska because the water depth is much greater than in the North Sea. Deep water necessitates that the tag's depth sensor have a greater range, which decreases depth resolution. Thus, tags used off Alaska have a depth resolution that is greater than the tidal range, therefore the tag cannot distinguish tidal fluctuations.

Another tagging method has been used to geolocate Baltic Sea cod (*Gadus morhua*) (Neuenfeldt[3]). This method is based on combined data of depth, temperature, and salinity obtained by electronic tags attached to cod. Hydrographic fields obtained from hydrodynamic modeling are used as a geolocation database to identify daily locations of fish by comparison with the environmental data collected by each electronic tag. Unfortunately, the tags that we used are not available with a salinity sensor and hydrodynamic models of the area are not accurate on the bottom (Hedstrom[4]).

Ambient light data collected by electronic tags may be used to calculate daily latitude and longitude estimates of fish. Geolocation by light has been implemented successfully on a variety of pelagic species to discern their daily position and movement patterns (Gunn and Block, 2001; Schaefer and Fuller, 2002; Itoh et al., 2003; Sibert et al., 2003).

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[3] Neuenfeldt, S., H.-H. Hinrichsen, and A. Nielsen. 2004. A method to geolocate eastern Baltic cod by using Data Storage Tags (DSTs), 14 p. Int. Coun. Explor. Sea CM / L : 06. Int. Coun. Explor. Sea, H.C. Andersens Boulevard 44-46, DK-1553, Copenhagen V, Denmark.

[4] Hedstrom, K. 2005. Personal commun. Artic Region Supercomputing Center, University of Alaska Fairbanks, PO Box 756020, Fairbanks, AK 99775.

However, no studies have been conducted to evaluate light-based geolocation estimates by tags attached to demersal fish, nor fish inhabiting high latitudes. Unfortunately, light levels in this system may be low and if the water is turbid, the light may be attenuated very quickly, thus hindering position estimates. Additionally, many demersal fishes inhabit a depth range where geolocation by light has not been evaluated at any latitude.

The goal of this study was to examine the applicability of ambient light geolocation estimation for demersal fishes in high latitudes. This was accomplished through the following objectives: 1) compare daily latitude and longitude estimates by two proprietary software types developed by the Wildlife Computers, 2) examine latitude and longitude estimates as a function of depth, and 3) examine *in situ* latitude and longitude estimates of Pop-up Archival Transmitting (PAT) tags attached to wild Pacific halibut.

Materials and methods

The Pop-up Archival Transmitting (PAT, Wildlife Computers, Redmond, WA, USA, version 2.0) tag is a miniature computer that is externally attached to a fish. The tag contains a clock and sensors that collect depth, temperature, and ambient light intensity data at user-specified intervals (Sibert, 2001). On a user-programmable date, the PAT tag releases from the fish, floats to the surface, and transmits summaries of the recorded temperature, depth, and light data to Argos satellites; the data are then retrieved by the investigator. If the tag is retrieved, the complete archival record of temperature, depth, and ambient light data may be obtained.

From October 2000 to March 2002, a pilot study was conducted to assess the feasibility of using PAT tags as a tool for identifying critical habitat of demersal fishes in high latitudes (Seitz et al., 2002, 2003). Geoposition estimates were made from light data collected in three experiments in which PAT tags were attached to: 1) Pacific halibut in outside aquaria, 2) a stationary mooring, and 3) *in situ* on wild Pacific halibut. The temperature and depth data from the wild Pacific halibut experiment and their Argos-based final locations have been reported previously (Seitz et al., 2003).

In the first experiment, two Pacific halibut were captured, transported live to outside aquaria at the Alaska SeaLife Center (Seward, Alaska; 60.099°N, 149.440°W) and tagged on 18 Oct. 2000 with PAT tags programmed to record light intensity every minute. The tags were retrieved on 01 May 2001, and the estimated longitudes and latitudes were compared to the known location of the aquaria.

A second experiment was conducted using a fixed mooring to examine latitude and longitude estimates as a function of depth. From December 2000 to April 2002, four PAT tags were attached to a stationary mooring line (the NOAA Alaska Observing System's "GAK-1" mooring) in Resurrection Bay, Alaska (59.852°N, 149.330°W) at depths of 27, 57, 96 and 146 m. These tags were attached to four different current vanes on the mooring line with light sensors facing up.

In a third experiment, to evaluate the performance of the light sensor and geolocation algorithm *in situ*, fourteen wild Pacific halibut (108–165 cm fork length) were captured, tagged and released in November 2000, March 2001 and July 2001 from a commercial longlining vessel in Resurrection Bay, AK, USA and off Cape Aialik, AK, USA (for

details, see Seitz et al., 2002, 2003). Light data were recovered from eight tags. PAT tags were externally tethered to each study animal by a piece of monofilament fishing line secured to a titanium dart that was inserted into the dorsal musculature of the fish. On a user-specified date and time, the PAT tag actively corroded the pin to which the tether was attached, thus releasing the tag from the animal. The tag floated to the surface and transmitted summarized data records via the Argos satellite system[5]. Upon popping-up, the tags' locations were determined from the Doppler shift of the transmitted radio frequency in successive uplinks (Keating, 1995). The endpoint position was the first Location Class (LC) estimate reported in the LC1-3 range, which all have error estimates <1.0 km.

The basis of light-based geolocation is the estimation of times of sunrise and sunset. Two proprietary programs developed by the Wildlife Computers, Argos Message Processor (AMP, version 1.01.0007) and Time Series Processor (TSP, version 1.01.0008), were used to extract daily sunrise and sunset times from the light intensity data. AMP identified daily sunrise and sunset times from light data transmitted through Argos satellites or directly from complete archival light records. TSP only could be used to identify sunrise and sunset times from complete archival light data of PAT tags that were physically recovered.

In the next phase, another Wildlife Computers program, Global Position Estimator (GPE, version 1.01.0005), used the sunrise and sunset times to calculate the tags' daily longitude and latitude. First, we rejected days with light level curves that did not exhibit

[5] Service Argos, Inc. (http://www.argosinc.com). [Accessed on: 13 December 2005.]

smoothly sloping light levels from high to low or low to high (Fig. 2.1). GPE was used to calculate longitude for the remaining data based on the local noon of the tag (mean of the sunrise and sunset times). Estimated longitude values that were not possible for a fish released in the Gulf of Alaska were rejected from the data set. For example, an impossible longitude was one that placed the tag on land or outside the published range of the Pacific halibut (i.e., to the west of Hokkaido, Japan (140°E) or to the east of Santa Barbara, CA, USA (117°W; Mecklenberg et al., 2002)). Once longitude was estimated, latitude was estimated by GPE, which used the "Dawn and Dusk Symmetry Method" (Hill and Braun, 2001; Musyl et al., 2001). Daily latitude estimates were the theoretical location of expected light levels that best matched the observed light levels measured by the tag. Latitude outliers were removed in a same manner as longitude outliers. For all three experiments, the number of days with geolocation estimates was defined as the days that produced latitude and longitude estimates, after "bad" light curves (Fig. 2.1) and outliers were removed.

For the tags with known positions in the tank and mooring experiments, we calculated bias and error magnitude based upon their true locations. Daily positional bias was calculated as the true position minus the estimated position (signed distance between positions), while daily error magnitude was the absolute value of the bias (distance between points). For the tank experiment, we pooled the data from the two tags. Mean error magnitudes of software types were compared using a two-tailed t-test. For the fixed mooring experiment, we calculated mean positional bias and mean error magnitudes for each tag and software combination. Mean biases were compared to a hypothetical bias of

zero using a two-way (tag and software) ANOVA model (SAS version 8, proc GLM). Mean error magnitudes were compared using an ANOVA with a Tukey-Kramer test (Kramer, 1956; SAS version 8 proc GLM). For both bias and error magnitude, the means are a measure of accuracy while the standard deviations are a measure of precision.

For wild fish, it was impossible to know the true daily position of each fish for the duration of the experiment. However, for three of the eight tags released on wild fish, geolocation estimates were produced in the first or last six days of deployment. Therefore, we compared the estimated positions of the tags for the six days immediately following release and the six days previous to recapture or reporting to Argos satellites. All three of these tags were physically recovered and TSP produced estimates for all tags. AMP only produced plausible estimates for one tag because other estimates were rejected as outliers. For each comparison, we calculated the mean bias and mean error magnitude assuming the fish was stationary (or nearly so) during the first and last six days of the deployment.

Results

All 14 tags, with the exception of one, functioned properly for the duration of the three experiments. The one exception, attached to a Pacific halibut *in situ*, was deployed for 234 days, but it only provided data for the first 42 days because the battery failed. Track durations for AMP (range: 42–479 days) were always equal to or greater than track durations of TSP (range: 42–348 days) because the memory for the archival data filled up before the summary data memory.

In the tank experiment, TSP was a better estimator of longitude than AMP. TSP rejected fewer outliers and produced a higher percentage of days with longitude estimates (89.5%) than AMP (82.9%). Additionally, the mean longitude error magnitude for TSP (1.0° ± 1.1° SD) was significantly smaller than that of AMP (2.0° ± 3.2° SD) (t=5.63, df=650, P<0.0001). Longitude errors were larger from late-fall to mid-winter in both tags when estimated by AMP, but not TSP. The mean longitude bias of TSP (-0.12° ± 1.5° SD) was significantly smaller than that of AMP (-0.64° ± 3.7° SD) (t=2.3, df=650, P=0.0215). TSP was not significantly biased while AMP had a significant mean longitude bias.

In the tank experiment, TSP also produced a higher percentage of days with latitude estimates (88.2%) than AMP (81.6%). However, there was not a significant difference in the mean latitude error magnitude between TSP (4.2° ± 5.1° SD) and AMP (4.4° ± 4.2° SD) (t=0.36, df=641, P=0.7155). The mean positional bias of TSP (–0.02° ± 6.7° SD) was not significantly different (t<0.0001, df=641, P =0.9730) than that of AMP (–0.08° ± 6.1° SD) and neither software type had a significant mean positional bias.

In the fixed mooring experiment, TSP was a better estimator than AMP of longitude. In general, the tags produced fewer longitude estimates as depth increased, and at each depth, TSP generated more estimates than AMP (Fig. 2.2). The mean longitude error magnitude for both programs increased at greater depth (Fig. 2.3). The mean error magnitude of AMP and TSP estimates were not significantly different at 27 m and 57 m (p>0.50), but AMP estimates quickly degraded starting at 96 m (Fig. 2.3). For the tags at 96 m and 146 m, the mean error magnitudes for TSP estimates were significantly smaller

($p<0.0001$) than the AMP estimates of the same tags. The mean longitude biases of both AMP and TSP were generally to the west (positive values) of the actual position of the tags except for AMP at 96 m (Fig. 2.3). In several cases, the mean biases were relatively small for both AMP and TSP, however both had large variances.

Like the longitude estimates in the fixed mooring experiment, the percentage of days with latitude estimates decreased at greater depths (Fig. 2.2). Unlike longitude, the ability of the tags to accurately estimate latitude was generally poor. Mean latitude error magnitude was significantly smaller for TSP than AMP at all depths, except 146 m (Fig. 2.3). The mean error magnitude for both AMP and TSP showed no relationship to increasing depth (Fig. 2.3). The mean latitude biases of the tags in the fixed mooring experiment were greater than the mean longitude biases and the biases by AMP were more variable than those of TSP (Fig. 2.3). Like longitude in the fixed mooring experiment, there were no latitude estimates at 146 m during the winter and spring. This time span was longer for latitude (242 days) than for longitude (165 days).

In the wild fish experiment, four tags reported only to Argos satellites and geoposition was estimated from summary data using AMP. The percentage of days with longitude estimates ranged from 0.0% to 2.3% (mean = 1.1% ± 1.0% SD) while the percentage of days with latitude estimates ranged from 0.0% to 1.5% (mean = 0.6% ± 0.7% SD). The other four tags were physically recovered and geoposition was estimated using both summary data for AMP and detailed data for TSP. For AMP, the percentage of days with longitude estimates ranged from 0.0% to 12.0% (mean = 5.8% ± 5.9% SD) while the percentage of days with latitude estimates ranged from 0.0 to 7.9% (mean =

3.4% ± 3.5% SD). For TSP, the percentage of days with longitude estimates was higher, ranging from 9.9% to 32.3% (mean = 19.7% ± 9.4% SD) while days with latitude estimates ranged from 9.9% to 26.6% (mean = 16.9% ± 7.2% SD).

The mean error magnitude of the longitude estimates for AMP (n=4; 2.98° ± 2.43° SD) was slightly larger than that of TSP (n=10; 2.23° ± 2.38 SD°). However, the mean error magnitude of the latitude estimates for AMP (n=4; 2.76° ± 1.59 SD°) was approximately half that of TSP (5.65° ± 4.11° SD). The mean longitude bias for AMP (2.95° ± 2.47° SD) was larger and to the east of that of TSP (-1.32° ± 3.04 SD°). The mean latitude bias was relatively small for both AMP (0.56° ± 3.50° SD) and TSP (0.10° ± 7.26 SD°), however both had large variances and thus the estimates were not precise. In several cases, the longitude estimates were within one degree of the true position and there did not appear to be a pattern of over or underestimating longitude.

Discussion

Geolocation estimation by light in high latitudes is equally effective as in lower latitudes. Similar to previous geolocation evaluations (Welch and Eveson, 1999, 2001; Musyl et al., 2001; Teo et al., 2004), longitude estimates were in general more accurate and precise than latitude estimates. Therefore, longitude estimation by light is a promising technique for discerning large-scale movement of demersal fishes in coastal Alaska, but latitude estimation using only light will not be adequate for these purposes.

This study was unique in testing light-based geolocation in depths greater than 60 m. The results demonstrate the importance of evaluating geolocation by light for the entire

depth range of the species of interest. Testing only in the near-surface waters is misleading because the percentage of days with estimates from the shallower tags was much greater than the percentage of days with estimates from the deeper tags, the depth which Pacific halibut most frequently inhabit (Seitz et al., 2003).

The accuracies of the longitude estimates in this study were comparable to those at lower latitudes and similar water depth. Errors are discussed in linear distance (Table 2.1) to account for the fact that a degree of longitude varies with latitude and to facilitate comparisons to previous studies. The longitude errors from the tank experiment were generally similar to the errors produced in a comparable experiment where tags were placed on a stationary mooring at a depth of 10 m (Welch and Eveson, 1999). The tags submerged at deeper depths in the fixed mooring experiment also showed similar longitude error magnitude to location estimates from tags in the offshore region of the Gulf of Alaska at 50° N, 145° W (Musyl et al., 2001; Welch and Eveson, 2001). The longitude biases were only slightly larger than those from tags on a stationary mooring near Hawaii (Musyl et al., 2001).

The minimum movement of a fish that is discerned by light-based geolocation in this experiment is the absolute sum of the error magnitude and bias. The sum of the error magnitudes and biases of TSP were generally smaller than those of AMP, therefore TSP was a better estimator of light-based geoposition than AMP and can be used to discern movement at a finer scale. The tank and fixed mooring experiments indicate that longitude estimation by TSP is able to discern movements of approximately ±200 km for depths as great as 150 m while AMP is able to discern east-west movements of

approximately ±350 km at 150 m deep. Geolocation by light will be able to discern the large-scale movements of Pacific halibut because this species performs spawning migrations of over 1100 km (Loher[6]). Additionally, with recovery rates as high as 50% in area-specific conventional tagging experiments (Kaimmer, 2000), TSP can potentially be used for a large portion of tag recoveries in future experiments.

At the largest scale, we are able to confidently discern whether the wild Pacific halibut in this study were in the Gulf of Alaska or Bering Sea. Individual estimates were subject to occasional large errors so caution should be practiced when using these estimates to represent the true position of the fish. Examining patterns in estimates is more useful for determining locations. To reach the Bering Sea (west of 157°W), a Pacific halibut would have to migrate from the Gulf of Alaska through False Pass (163.5°W), which is the eastern-most connection between the two areas. The wild Pacific halibut in this study appear to have remained within the Gulf of Alaska, as fewer than 5% of the longitude estimates were to the west of 163.5°W, and those appear to be erroneous because adjacent estimates do not consistently corroborate them. Trends in longitude estimates do not provide sufficient evidence to suggest that any of the wild Pacific halibut swam to the Bering Sea.

A variety of uncontrollable factors can cause intrinsic and extrinsic errors in geolocation estimates. The predominant source of intrinsic error is refraction in the earth's atmosphere that is caused when light travels through the atmosphere and is bent

[6] Loher, T. 2005. Personal commun. Int. Pac. Halibut. Comm, PO Box 95009, Seattle, WA 98145-2009.

by air and other molecules (Schaefer and Liller, 1990). This error limits the absolute accuracy of the estimates to a constant 0.32° longitude and a minimum of 0.7° latitude (Hill and Braun, 2001). Extrinsically, light levels may be drastically influenced by changing external conditions such as waves, water turbidity, diving behavior of the animal, biofouling, and cloud cover (Metcalfe, 2001). In particular, the Alaska coastal region frequently experiences large changes in weather systems that change cloud cover and sea-state on a daily, or even hourly, basis. One final consideration for errors is that accurate location estimates rely on unobstructed horizons. If the horizon is obstructed, such as by the mountains surrounding the coast of Alaska, it alters the time(s) of apparent sunrise (and sunset), thus affecting geolocation estimates. The tank experiment was conducted in a deep, north-south fjord whose walls obstructed the horizon and the fixed mooring experiment was adjacent to an island on the east, and steep coastal mountains to the west. Undoubtedly, these false horizons accounted for part of the errors and bias.

One shortcoming discovered in the fixed mooring experiment was a conspicuous gap in longitude and latitude estimates from December to June at 146 m. This six-month gap was probably the result of low ambient light levels during the winter associated with high latitudes. It is unknown why the gap lasted into the summer when ambient light drastically increased. However, with respect to practical application in studies of Pacific halibut migration, light-based geolocation estimates will capture some individual migrations to the spawning grounds as some Pacific halibut begin migrating in October and arrive on the continental slope by early November (Seitz et al., 2003).

We may be able to increase the number of location estimates with some fine-tuning of both software types. Several days were rejected because of poor light readings. However, some days had smoothly sloping sunrise and sunset events that appeared to be sufficient for accurate geolocation estimates, but the software misidentified sunrise and sunset. This typically occurred because there were occasional aberrant light readings. The geolocation software identified these as sunrise, sunset or both, thus they gave bogus position estimates. There is an option to override these aberrant sunrise and sunset times when using TSP because the software allows manual selection of sunrise and sunset. For this study, we opted not to do this because we did not want to introduce subjectivity into sunrise and sunset times. We suggest that the software be modified by the manufacturer to select the next best times for sunrise and sunset so the investigator may reject aberrant light readings and yet allow the software to objectively choose sunrise and sunset.

In future studies, we hope to improve geoposition estimates by statistically filtering (Sibert et al., 2003) or smoothing longitude estimates and incorporating additional sensor data. For example, in conjunction with light data, tag-measured sea-surface temperature (SST) can be compared to remotely-sensed SST, to significantly improve geolocation estimates (Teo et al., 2004). In the case of demersal fish that rarely, if ever, visit the sea surface, maximum daily depth can be used as representative of the total water depth in the region. We can compare the maximum daily depth sampled by an electronic tag to existing bathymetry data to estimate possible daily positions of the fish. We can then combine the geolocation by light-level information and the depth information to yield a most plausible track of daily positions.

Accurate description of the movement of fish is the cornerstone of sound management plans for ensuring sustainable fisheries in the future (Hunter et al., 2003). Longitude estimation by light may be used to examine large-scale movements of demersal fish in high latitudes. There are several types of electronic tags, with some designed for fish as small as 15 cm (Arnold and Dewar, 2001). Using this technique, we can describe large-scale spatial dynamics and migration of several commercially important demersal fish species.

Acknowledgments

This project was made possible through the expertise of: Capt. Harold Kalve of the F/V *Rocinante* during fishing operations; Dave Douglas, Dan Mulcahy DVM, and Julie Meka of USGS-Alaska Science Center; Susan Ingles, Richard Hocking, Pam Parker, Brian Mullaly, Jessica Dunning and the staff at Alaska Sea Life Center; and Tom Weingartner, David Leech and the crew on the R/V *Alpha Helix* from the University of Alaska Fairbanks. A special thanks to Dr. Devin Johnson for statistical assistance. Partial funding for this project was provided by the Exxon Valdez Oil Spill (EVOS) Trustee Council (Restoration Project 478) and the U.S. Geological Survey-Alaska Science Center. The Gulf of Alaska (GAK) 1 mooring is funded by the EVOS Trustee Council under a separate grant (Restoration Project 340). The findings presented by the authors are their own and not necessarily the position of the EVOS Trustee Council.

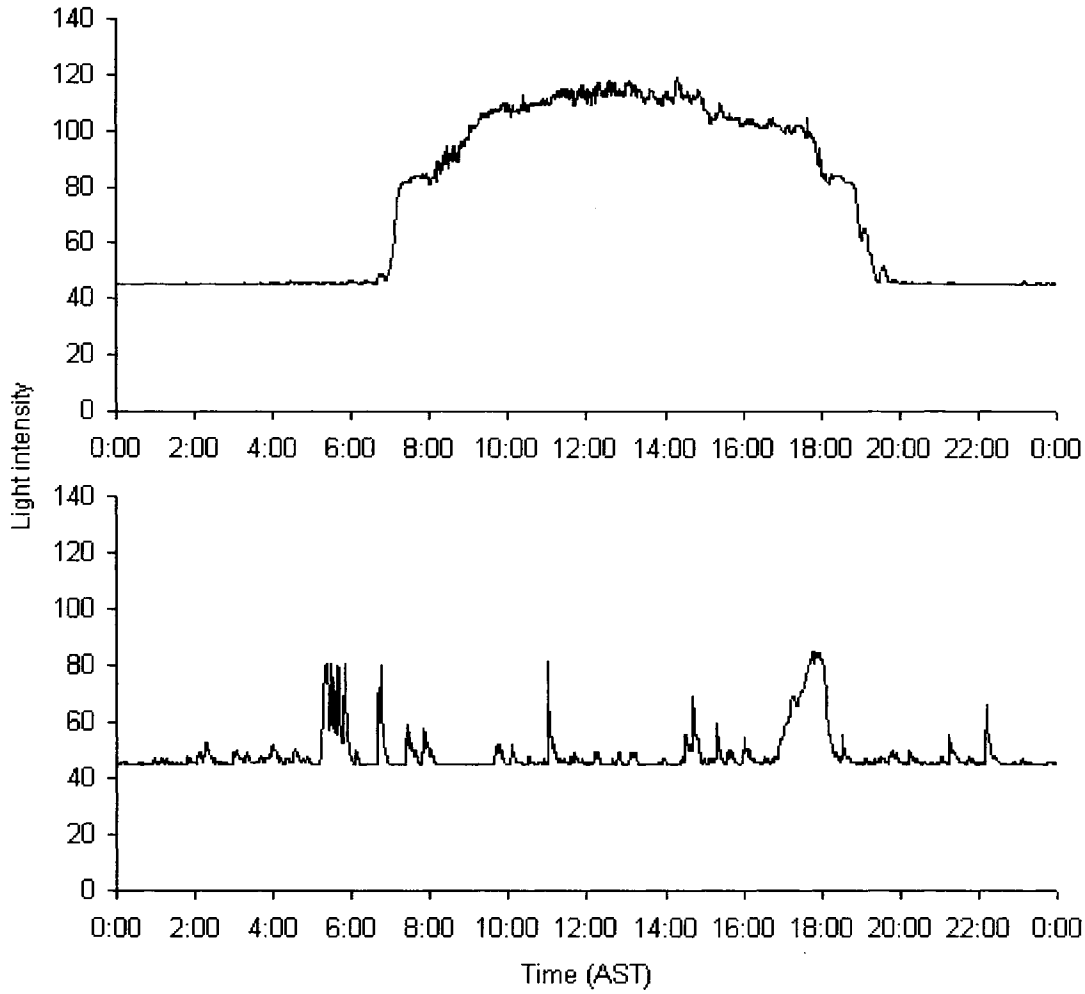

Figure 2.1. Examples of "good" and "bad" light curves. "Good" light curves (top panel) have smoothly sloping sunrise and sunset events. "Bad" light curves (bottom panel) do not have smoothly sloping sunrise and sunset events, and produce outlying longitude and latitude estimates. The "good" light curve is from 2 March 2001 and the "bad" light curve is from the same tag on 10 March 2001.

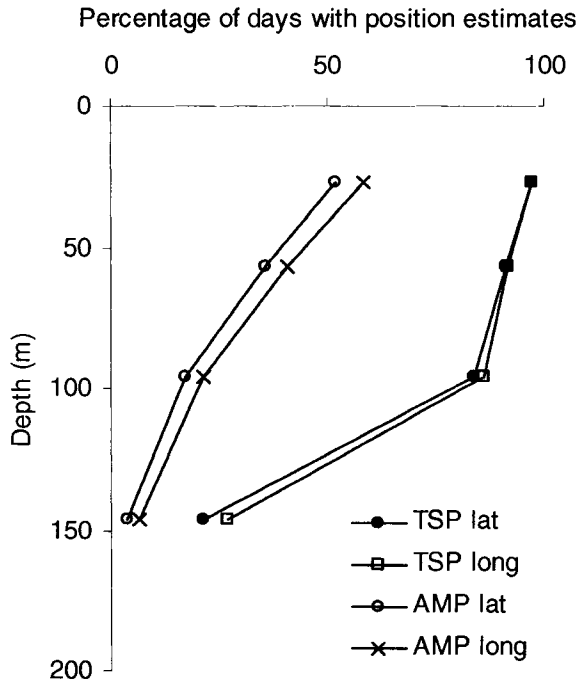

Figure 2.2. Percentage of days with longitude and latitude estimates as a function of depth in the fixed mooring experiment. Two programs, Argos Message Processor (AMP) and Time Series Processor (TSP), were used to calculate daily longitude and latitude.

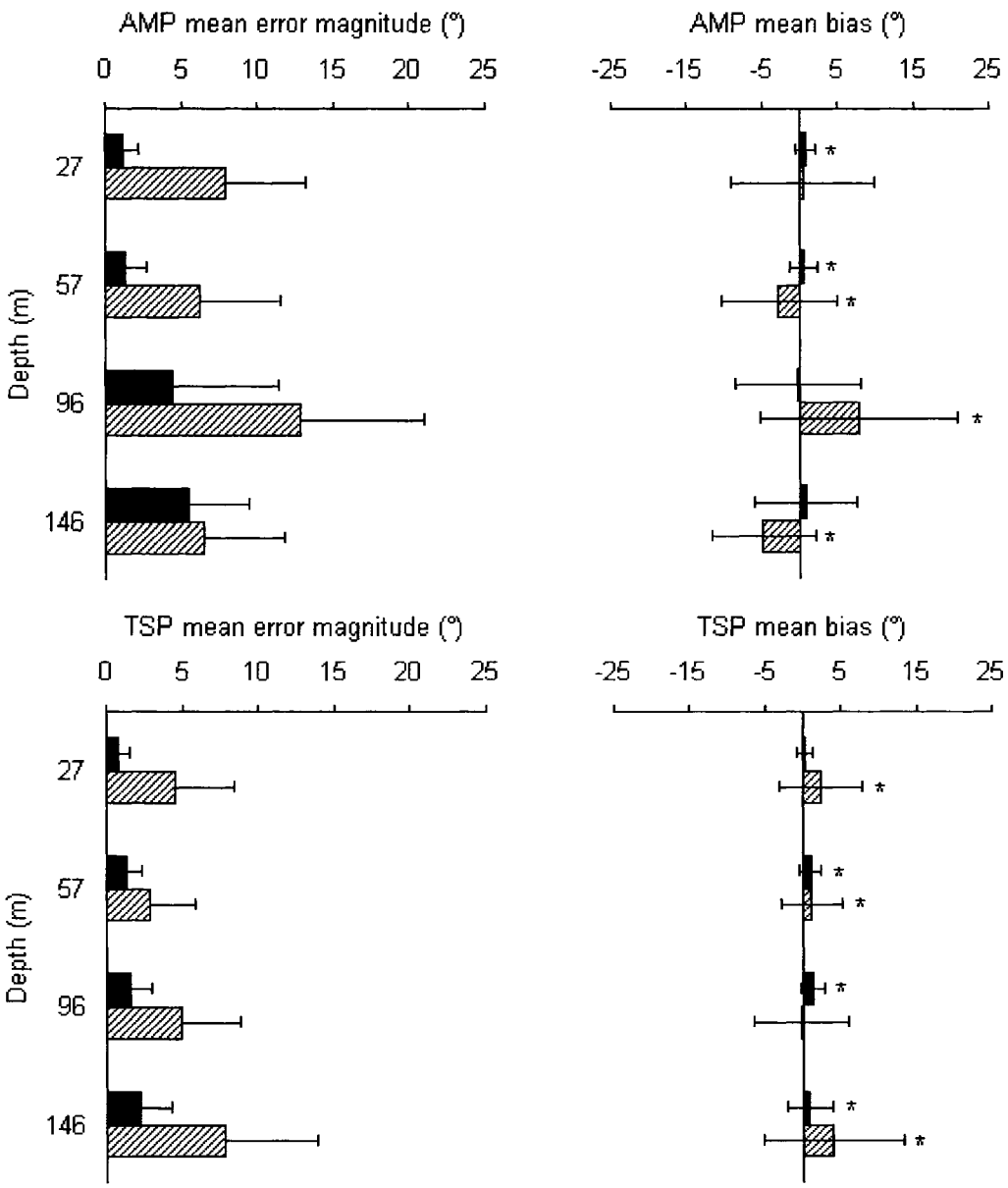

Figure 2.3. Mean (±SD) positional errors and bias in the fixed mooring experiment. Two programs, Argos Message Processor (AMP) and Time Series Processor (TSP), were used to calculate daily longitude (black bars) and latitude (hatched bars). Asterisks (*) indicate mean positional biases significantly different than zero tested by two-way ANOVA. A negative bias indicates that a position estimate was either north or east of the known position, and a positive bias indicates that a position estimate was either south or west of the known position.

Table 2.1. Linear distance of mean error magnitude for the tank, fixed mooring, and wild fish experiments. Longitude and latitude were calculated from light intensity data collected by Pop-up Archival Transmitting tags by two programs, Argos Message Processor and Time Series Processor. Mean error magnitude was calculated by averaging the absolute value of the true position minus the estimated position of the tag for each day of the experiment. Total error was the vector distance from the known location of the tag when longitude and latitude errors were combined. The great circle formula was used to convert angular errors to linear distances.

			AMP			TSP		
Experiment	Tag	Depth (m)	Longitude (km)	Latitude (km)	Total error (km)	Longitude (km)	Latitude (km)	Total error (km)
Tank	00-0740	0	139.1	500.9	519.8	62.9	500.9	504.8
Tank	00-0741	0	83.5	480.8	488.0	48.4	445.2	447.8
Mooring	00-0822	27	66.2	873.7	876.2	41.7	505.3	507.0
Mooring	00-0826	57	74.6	696.8	700.7	74.6	310.5	319.4
Mooring	00-0806	96	241.5	1421.3	1441.7	89.6	540.9	548.3
Mooring	00-0824	146	299.3	726.8	786.0	123.5	871.5	880.2
Wild fish	All tags	90–202	165.8	307.2	362.6	124.1	628.9	392.0

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CHAPTER THREE

Minimum distance dispersal model of demersal fish in the Gulf of Alaska[1]

ABSTRACT

A method of estimating daily location is needed for demersal fishes in northern latitudes because seasonally low ambient light levels and habitation of deep water (>200 m) restrict geolocation by light. Using data recovered from electronically tagged demersal fish, we constructed a minimum-distance dispersal model by identifying locations where bathymetry data conformed to the fishes' daily maximum depth. Each track was started at the tag recovery location. An algorithm searched bathymetry data within radii specified by the estimated swimming speed for the species and determined all locations where the ocean depth matched the maximum depth of the fish. The location that was closest to the release location of the tagged fish in the summer was selected as the solution. Iterations were repeated until the model returned the fish to its initial release location. The results were sensitive to swimming speed and time elapsed between depth readings. The model was able to estimate the minimum distance traveled and hypothetical movement paths of the fish as it foraged on the summer feeding grounds and during seasonal dispersal. Dispersal distances calculated by the model represented a 20% to 10-fold increase over the straight line distance between the beginning and end points.

[1] A.C. Seitz, D.C. Douglas, B.L. Norcross, and J.L. Nielsen. In preparation. Minimum-distance dispersal model of demersal fish in the Gulf of Alaska. Ecological Modelling.

The minimum-distance dispersal model presents an alternative method to light-based geolocation for demersal fishes and provides dispersal information about these fish, even in remote environments that are difficult to sample, like the Gulf of Alaska.

Introduction

Many marine fish species undertake seasonal movements associated with dispersal from feeding areas to spawning areas (Harden Jones 1968). For example, adult Pacific halibut (*Hippoglossus stenolepis*) feed during the summer on the continental shelf, disperse to the continental slope in late fall to spawn during the winter, and in early spring disperse back to the same summer feeding grounds each year (Dunlop et al. 1964, Best 1981). The spawning season occurs from early November to late March on grounds concentrated along the continental slope at depths from 200 to 500 m (IPHC 1998), while emerging data from electronic tags suggest that spawning likely occurs to depths of 800 m (Seitz et al., 2003; Loher and Seitz, 2006; Chapter Four). This general pattern has been described by several experimental fishing and conventional tagging studies (IPHC 1998), but detailed description of these movements is a challenging task because of the vast size and relative inaccessibility of the marine environment.

New methods using information collected by electronic tags, which contain miniaturized onboard computers, are providing more detailed movement description of demersal marine fishes (see review in Arnold and Dewar, 2001). In the Gulf of Alaska, geolocation by light data collected by electronic tags is currently the most feasible

method for obtaining daily location estimates of demersal fish (Chapter 2). However, geolocation by light has precision and accuracy shortcomings in longitude and latitude estimates that limit its effectiveness in providing daily location estimates and migration pathways of fish in the North Pacific Ocean (Chapter 2). Generally, error magnitude increases with depth, with latitude errors much greater than longitude errors. For longitude, the accuracy is ±200 km at 150 m depth; therefore geolocation by light is only able to discern basin-scale movements, but provides a feasible method for providing scientific inference on large-scale population structure in demersal fishes in high latitudes. Additionally, from November to March, light penetration past 100 m water depth is insufficient to be detected by the light sensor, thus leaving a winter gap in geolocation estimates.

Therefore, the objective of this study was to develop an alternative method of identifying locations and migration pathways of demersal fish in the Gulf of Alaska based on daily maximum depth. To accomplish this, we constructed hypothetical movement paths by identifying locations where bathymetry data conformed to the daily maximum depth recorded by externally attached electronic tags. In this study, we used Pacific halibut because we have depth data from fish that were electronically tagged in experiments conducted in the Gulf of Alaska (Seitz et al. 2002 and 2003). The model presented here avoids the limitations of geolocation by light and estimates daily position at a finer scale.

Methods

Gulf of Alaska bathymetry data were obtained from the Sea-Air-Land Modeling and Observing Network (SALMON) Project, at the Institute of Marine Science, University of Alaska Fairbanks (http://www.ims.uaf.edu/salmon/bathymetry/bathymetry.html). The dataset was derived from National Oceanographic Data Center soundings point data for coastal areas and ETOPO5[2] data on a 5 minute latitude/longitude grid for offshore areas. For both sources, data were translated to North American Datum of 1983 (National Oceanic and Atmospheric Administration 1986).

The depths of fish were measured by Pop-up Archival Transmitting (PAT, Wildlife Computers, Redmond, WA, USA, version 2.0) tags in the Gulf of Alaska. These tags were deployed in a pilot study that was conducted to assess the feasibility of using PAT tags as a tool for identifying critical habitat of demersal fishes in high latitudes (Seitz et al. 2002, 2003). In the pilot study, each PAT tag was given a unique identification number, which are used in this study to allow reference to the full data record of each tag reported in previous publications (Seitz et al. 2002; 2003). PAT tags were externally tethered to each study animal and contained a clock and sensors that collect depth, temperature, and ambient light intensity data at user-specified intervals. On a user-programmable date, the PAT tag released from the fish, floated to the surface, and transmitted summaries of the recorded temperature, depth, and light data to Argos satellites. When the tags reached the water surface, locations were determined from the

[2] Data Announcement 88-MGG-02, Digital relief of the Surface of the Earth. NOAA, National Geophysical Data Center, Boulder, Colorado, 1988. (http://www.ngdc.noaa.gov/mgg/global/etopo5.HTML)

Doppler shift of the transmitted radio frequency in successive uplinks (Keating 1995). The endpoint position was the first Location Class (LC) 1-3 estimate, which all have error estimates <1.0 km (Loher and Seitz 2006).

Using the bathymetry and fish depth data (Fig. 3.1), we constructed a minimum distance dispersal model to describe locations and dispersal pathways of demersal fish. The model relied on four key assumptions: 1. The maximum depth recorded within a 12 hour summary period corresponds to benthic behavior in which the fish was on or near the ocean floor; 2. Fish were released and remained at summer feeding grounds for as long as possible; 3. End point was fish's spawning location; and 4. Fish traveled the minimum distance between locations, while satisfying depth requirements. Therefore, fish were not modeled to have moved horizontally unless mandated by a change in depth. As such, dispersal distances estimated by the model are expected to be conservative relative to the total amount of movement experienced by individuals during their time at liberty.

Modeling the location and movement path was an iterative process that started at fish's final depth and location. An ArcINFO algorithm searched the bathymetry database within specified radii for all locations where the ocean depth matched the maximum depth recorded by the PAT tag during the previous summary period (Fig. 3.2). The radii searched for possible locations were specified as:

$$R = T_D * S_S$$

where R is the search radius, T_D is the elapsed time between depth readings (i.e., the length of summary period), and S_S is swim speed. Ideally, T_D was 12 hours which is the

period we specified for data summaries. However, because of incomplete satellite transmission to Argos (Seitz et al. 2002), data summaries for 12 hour periods were occasionally missing and T_D was a larger multiple of 12 hours. The location that was closest to the summer release location was selected as the solution. The model did not attempt to resolve a movement path between locations, therefore no assumptions were made about the depth and location of the fish during the interval between depth records. The search radius of the next model iteration was started at the solution to the previous iteration, but the model selected the ending location based on the ending depth. Iterations continued until the fish reached its tag and release location.

The model was started at the fish's final location and run in reverse chronology to bias the movement towards the latter portion of the depth data. Several Pacific halibut in another study remained on summer feeding grounds into late fall and even winter, suggesting that the fish probably remain on summer feeding grounds for as long as possible before moving to winter spawning grounds (Chapter 4). We were able to start the model at the fish's release location and run it in forward chronology, but this biased the movement towards the earlier portion of the data and the fish arrived near the winter grounds shortly after release in the summer which is probably unrealistic (St-Pierre 1984).

Because there are no published estimates of swimming speed for Pacific halibut, swim speeds of 1.5, 2.0, 3.0, 3.5 and 7.0 $km \cdot hr^{-1}$ (0.4 to 1.8 body $lengths \cdot sec^{-1}$) were tested on fish 01-0047. The lower limit was similar to swim speeds of smaller confamilial flatfish species (Buckley and Arnold 2001), while a likely unrealistic upper

limit was similar to swim speeds of equally sized Pacific bluefin tuna (*Thunnus orientalis*; Marcinek et al. 2001), one of the fastest marine fish species.

Dispersal was classified into two types (Fig. 3.3): "one-way" and "roundtrip." One-way dispersals were those that modeled travel on the summer feeding grounds and to the winter spawning grounds (fish 01-0047, 00-0737b, 00-0741 and 00-0819; Fig. 3.3). In these model-runs, the area available to the fish was unrestricted as they had access to any location in the Gulf of Alaska. Roundtrip dispersal modeled travel on the summer feeding grounds and the winter spawning grounds, and the dispersal between these locations. Currently, we have recovered only one tag that was attached to a Pacific halibut during a roundtrip dispersal (fish 00-0737a; Fig. 3.3). For the roundtrip dispersal, we ran an unrestricted model in which the fish had access to any location in GOA and a restricted model in which the fish was prohibited from entering Prince William Sound (Fig. 3.3). Prince William Sound has appropriately deep water to satisfy depth requirements of the fish during the winter and is closer to the release location of fish 00-0737a than the offshore continental slope. We ran the restricted model to determine where the fish would travel if it was not able to enter Prince William Sound, because there have been very few Pacific halibut tagged in the Gulf of Alaska that were recovered in Prince William Sound (Skud 1977).

The distance traveled in a model iteration was the straight-line distance between the initial and final locations of that iteration. For all modeled dispersals, we calculated the distance traveled while on the feeding grounds and during dispersal to spawning grounds. For roundtrip dispersal, we additionally calculated the distance traveled while on the

winter grounds, during dispersal back to feeding grounds, and while back on the feeding grounds for both the restricted and unrestricted models.

Results

Swimming speed

The model failed to find bathymetric solutions at 1.5 km·hr^{-1} and 3.0 km·hr^{-1} (Fig. 3.4). In these cases, the model moved the fish to an intermediate location, but could not find an ocean depth that matched the tag depth within the given radius of travel. At 1.5 km·hr^{-1}, the rate was too slow for the fish to ascend a shallow sill in front of the deeper waters of its destination. At 3.0 km·hr^{-1}, the fish was unable to move from the deep continental slope water to the shallower shelf water. These swim speeds were considered implausible and were rejected.

The model was able to describe the fish's movement from its tagging location to its final location at 2.0 km·hr^{-1}, 3.5 km·hr^{-1}, and 7.0 km·hr^{-1}. The fish's distance traveled while on its feeding ground was considerably greater at 7 km·hr^{-1}, than at 2.0 and 3.5 km·hr^{-1} (Fig. 3.4) because on several instances the model moved the fish into Prince William Sound for brief periods before returning to its release area. Because Pacific halibut are thought to remain in a limited summer feeding range and do not undertake long-distance foraging trips (Hooge and Taggart 1993), a swim speed of 7.0 km·hr^{-1} was considered implausible and rejected. 2.0 km·hr^{-1} (0.34 to 0.51 lengths·sec^{-1}) was selected

as the swimming speed of Pacific halibut because this speed is similar to the swimming speed of the most closely related confamilial species, the plaice (*Pleuronectes platessa*), for which there are published swimming estimates of adult fish (Buckley and Arnold 2001). Generally, shorter fish like plaice are unable to maintain equal average swim speeds of longer fish like Pacific halibut, and plaice are approximately 25–35% of the length of the fish in this study. However, the published swim speeds of plaice are instantaneous speeds while the swim speeds of Pacific halibut in the present model were averaged over 12 hours. When taking into account the fact that instantaneous speeds will be higher than speeds averaged over an hour, we believe that the instantaneous cruising speed of the plaice approximates the average speed of a Pacific halibut.

Dispersal distance

The dispersal of five fish was modeled using the minimum-distance model, of which four were one-way dispersals and one was a roundtrip dispersal. These fish ranged in length from 108 to 165 cm and were located 20 to 358 km from their release sites after 135 to 244 days at-liberty (Fig. 3.3).

For the one-way dispersals, their total minimum travel distances were greater than the straightline distances between their release and recovery sites (Fig. 3.5). The total minimum travel distance, including travel on the summer grounds and to the winter grounds, varied from 125 to 888 km, representing an 11% to 148% increase over their

horizontal displacement. The minimum distance traveled while on the feeding grounds varied considerably, even though these fish inhabited the summer grounds for approximately the same amount of time. For three fish, the distance traveled during the summer feeding season was less than that during the seasonal dispersal to the winter grounds. In contrast, one fish traveled more on the summer feeding grounds than during its seasonal dispersal to winter grounds. We were unable to estimate a minimum distance traveled on the winter grounds because the model is run in reverse chronology which causes the fish to arrive at the winter grounds on the last day of the model run.

For the fish whose roundtrip dispersal was modeled, the total distance traveled far exceeded its horizontal displacement of 20 km (Fig. 3.6). Under the unrestricted scenario, the fish swam at least 1032 km, while under the restricted scenario it swam at least 650 km. The distance traveled when on the winter grounds was greatest among all the movement stages for both the unrestricted and restricted scenarios (Fig. 3.6).

Discussion

The minimum distance dispersal model is an alternative method of studying the movement of demersal fish in the Gulf of Alaska. This region supports several commercially valuable demersal fisheries, but studying the fish is particularly challenging because they typically occupy inhospitable and remote environments. The minimum distance model provides fine-scale inference on fish dispersal in the Gulf of

Alaska by producing daily locations and distance traveled while avoiding the limitations of alternative methods such as geolocation by light (Chapter 2).

The minimum distance dispersal model is an improvement over calculating dispersal distance from only beginning and end point data, the latter of which almost surely underestimates the distance traveled by fish. For one-way seasonal dispersal, this is intuitive because it is unlikely that fish swim in a straight line from their feeding grounds to their spawning grounds. The minimum distance dispersal model provides a quantitative and theoretically conservative estimate of the curvilinear travel distance between the seasonal locations. In the case of Pacific halibut, the curvilinear minimum dispersal distance to the winter grounds was approximately 20–40% greater than the straight line distance.

The model is perhaps even more informative for estimating minimum distance traveled by fish that complete a roundtrip dispersal circuit. This fish in this study must have traveled farther than its horizontal displacement of 20 km to attain a maximum depth of 502 m (Seitz et al. 2003). The model estimated a total seasonal dispersal distance (movement between summer and winter locations and vice-versa) of at least 209 km, representing a 10-fold increase over the straight line distance between its tagging and recovery locations. This increase does not even include the fish's likely movements while on the summer and winter grounds.

The minimum distance dispersal model is able to estimate a lower dispersal threshold while foraging on the summer grounds in addition to seasonal dispersal distance. Due to the construction of the model and the constraint that horizontal displacement could only

be associated with changes in depth, the model was unable to detect any dispersal for one of the fish during the feeding season. In contrast, three Pacific halibut generated considerable dispersal while on the feeding grounds; these fish traveled a distance that was 10–50 times greater than the fish that showed limited dispersal during the same time. For Pacific halibut, previous research in an enclosed fjord indicates that they may occupy and forage in limited home ranges (Hooge and Taggart 1993). Whether the fish in this study had a home range and simply undertook long distance foraging trips, or they did not have a limited home range is unknown.

The predicted movement paths are likely more accurate for one way dispersals than roundtrips because the exact location of the latter fishes' winter grounds are unknown. For the one way dispersals, the model assumptions dictated that they moved to deeper water on the slope adjacent to their summer grounds and then traveled in this deeper water to their winter grounds. This pattern was chosen because it is in agreement with the longitude record of a Pacific halibut in another study in the Gulf of Alaska (Fish S-138; Loher and Seitz 2006), which is the only fish in the region that dispersed a sufficient distance for the longitude estimates to show a movement trend. This fish's depth increased before the longitude estimates moved, indicating an offshore movement before swimming along the continental slope which is similar to the fish in this study. For the fish that undertook a roundtrip dispersal, the model predicts that the fish will move to the closest location that satisfies depth requirements. This prediction is not necessarily true as all of the one-way dispersals in this study traveled considerably farther than the first location that satisfied the winter depth requirements of the roundtrip dispersal.

The accuracy of movement paths of roundtrip dispersers may be improved by restricting the area available to the fish. The model indicated that the roundtrip disperser moved to Prince William Sound during the winter rather than the continental slope. This is possible, but we believe this is unlikely because very few Pacific halibut tagged in the Gulf of Alaska in previous studies moved into Prince William Sound (Skud 1977; Seitz et al. 2003; Loher and Seitz 2006). Furthermore, the distance traveled while on the predicted winter ground in Prince William Sound appeared artificially high as the movement during this time was much greater than during the dispersal phases and the summer feeding season. When the area of movement was restricted, the model predicted that the fish would move to the offshore continental slope, which is consistent with other Pacific halibut (Skud 1977; Seitz et al. 2003; Loher and Seitz 2006). Additionally, the predicted distance traveled while on the offshore winter grounds in the restricted scenario was greatly reduced and more consistent with the distance traveled during the other dispersal phases.

The minimum distance dispersal model relied on four assumptions of Pacific halibut behavior that may greatly influence the model results. First, the deepest depth record in each summary period probably represented bottom depth. Pacific halibut are a demersal fish adapted for life on the benthos. The fish are known to leave the sea floor occasionally for the pelagic realm, but we have no evidence that these forays exceed 12 hours (Seitz et al. 2003). Therefore, the fish were most likely near or on the bottom for some period of time within 12 hour summary periods, which likely corresponded to the maximum depth. Second, we ran the minimum-distance model in reverse chronology to

bias the movement of the fish toward the latter portion of the data record, i.e., the arrival on the spawning ground. By delaying the arrival on the spawning grounds, the fish would maximize energy reserves prior to spawning by feeding as late into the summer season as possible. We have no way of validating the exact timing of movement, but the model probably approximates the dispersal timing sufficiently, as data available to date suggest that Pacific halibut remain on summer feeding grounds late into fall before moving to winter spawning grounds (Chapter 4). Third, the final locations of several of the one-way dispersers coincide with major spawning grounds of Pacific halibut in the central Gulf of Alaska (St-Pierre 1984). Therefore, the end points used in the minimum distance model probably approximate the fishes' final spawning locations. Fourth, to minimize energy expenditure during their dispersal to the spawning grounds, fish probably travel a minimum distance between the summer feeding grounds and their winter spawning grounds (Harden Jones 1968). Pacific halibut do not necessarily swim to the winter grounds that are closest to their summer feeding grounds as evidenced by a fish that swam past seven major spawning grounds during its seasonal dispersal (Loher and Seitz 2006), but they probably minimize the distance traveled on the way to their final destination.

There is no indication that these assumptions were violated, with the exception of one fish, 00-0741. This fish may not have stayed on the feeding grounds at its release location as long as possible before dispersing to the winter grounds. Its estimated dispersal distance on the feeding grounds was at least 51% larger than the other fish, which was probably artificially high. This was most likely caused by the model

permanently moving the fish from its release site to another location of similar depth within the radius of possible movement from its release location. During the feeding season, the fish frequently visited relatively deep water. If this new summer location were closer to the relatively deep water than the release site, the model would overestimate distance traveled by repeatedly moving the fish back to its release location instead of the new location.

The results of the model were highly sensitive to swimming speed because of the irregular bathymetry of the continental shelf of the Gulf of Alaska. This region contains several shallow areas surrounded by relatively deep troughs that are oriented perpendicular to the shelf (Weingartner 2005). If the swimming speed was too slow, the model was unable to move the fish over shallow locations. For example, if an *in situ* tagged fish moved over a shallow area in 36 hours at 2.0 $km \cdot hr^{-1}$, the tag would yield three relatively shallow depth readings over a span of 72 km. However, if we model the swim speed at 1.5 $km \cdot hr^{-1}$, the modeled fish would experience the same amount of depth readings over a span of only 54 km. The modeled fish would then have to swim to relatively deep water to satisfy the depth requirements of the tag. However, a slow swim speed would not allow the fish to move off the shallow location in time to experience greater depths as required by the tag record. In contrast, if the speed was too fast, the model probably moved the fish more than it actually swam, thus resulting in inflated dispersal estimates. For example, if the modeled speed was unrealistically high when performing iterations in reverse chronology to find the dispersal from the winter area to the summer area, the modeled dispersal time would be less than the actual dispersal time.

If during this dispersal time, the fish moved over an area that had equivalent depth to its summer feeding area, the model would erroneously place the fish on its summer feeding area. This would cause the fish to be on the summer feeding grounds when it was still actually on the continental slope. When the fish's depth increased again before moving onto the shelf, the model would have to move the fish back onto the slope from the summer feeding grounds. When this happens repeatedly, the modeled distance traveled would be artificially high.

The model results were also sensitive to time elapsed between depth readings. Incomplete satellite transmission of the data can cause gaps in the depth record (Seitz et al. 2002) that create longer elapsed time intervals. As the time intervals increase, the number of possible bathymetric matches increases as more area becomes available. An extreme case was fish 00-0819, in which the time interval immediately before the tag reported its final location was 96 hours. The fish's horizontal displacement was only 112 km, so the fish was able to swim this distance in less than the final time interval. Thus, the model was unable to provide any estimated swimming path from the fish's starting and end locations.

With some future refinements, we may be able to improve the minimum distance dispersal model. Most importantly, swimming speeds need to be ascertained, either *in situ* using electronic tags, video from a Remotely Operated Vehicle or submersible, or in a laboratory using a swimming flume. It is also possible that the fish use different swimming speeds for foraging on the summer grounds and migrating to the winter grounds. This could be incorporated into the model and would probably be more

accurate, but we did not do this because we did not have any published estimates of Pacific halibut swimming speeds with which to start. To reduce uncertainty in our positions, we hope to compare bottom temperatures collected simultaneously by the tag to temperatures predicted by hydrographic models. Currently, we are unable to achieve this goal because hydrographic models of the Gulf of Alaska do not accurately portray the bottom temperature (K. Hedstrom, University of Alaska Fairbanks, pers. comm.).

The minimum distance dispersal model presented here represents a first step in the development of an alternative to light-based geolocation for demersal fishes to provide dispersal information about these fish, even in remote environments that are difficult to sample, like the Gulf of Alaska. Given the economic importance of several demersal fish species in the region (Woodby et al. 2005) such as Pacific cod (*Gadus macrocephalus*), sablefish (*Anoplopoma fimbria*), lingcod (*Ophidian elongates*) and rockfish (*Sebastes* sp.), and the difficulty in sampling them during certain times of the year, these methods represent an important advance in describing fish movement.

Acknowledgments

This project was made possible by: Capt. H. Kalve of the F/V *Rocinante* during fishing operations and Derek Wilson of the United States Geological Survey-Alaska Science Center (current address: Oregon Department of Fish and Wildlife) for tagging assistance. Partial funding for this project was provided by the Exxon Valdez Oil Spill Trustee Council, the U.S. Geological Survey–Alaska Science Center and the University of Alaska

Fairbanks School of Fisheries and Ocean Sciences. The findings presented by the authors are their own and not necessarily the position of the EVOS Trustee Council.

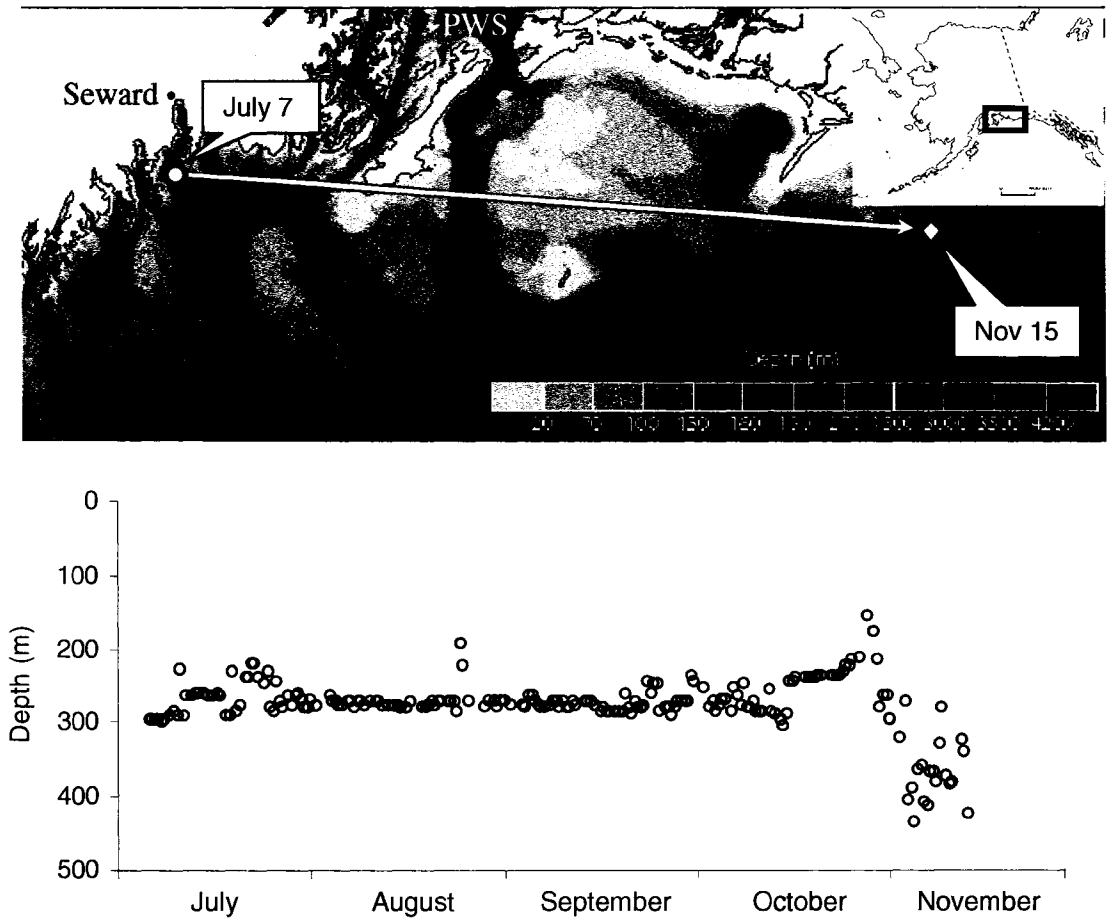

Fig. 3.1. Example of raw data used in the minimum distance dispersal model (fish 00-0737b; from Seitz et al. 2003). Upper panel – start (O) and end locations (◇) for a Pacific halibut in the northcentral Gulf of Alaska with straight line path between locations. PWS = Prince William Sound. Lower panel – maximum depth in 12-hr segments measured by a Pop-up Archival Transmitting tag. Minor data gaps may exist due to incomplete satellite transmission.

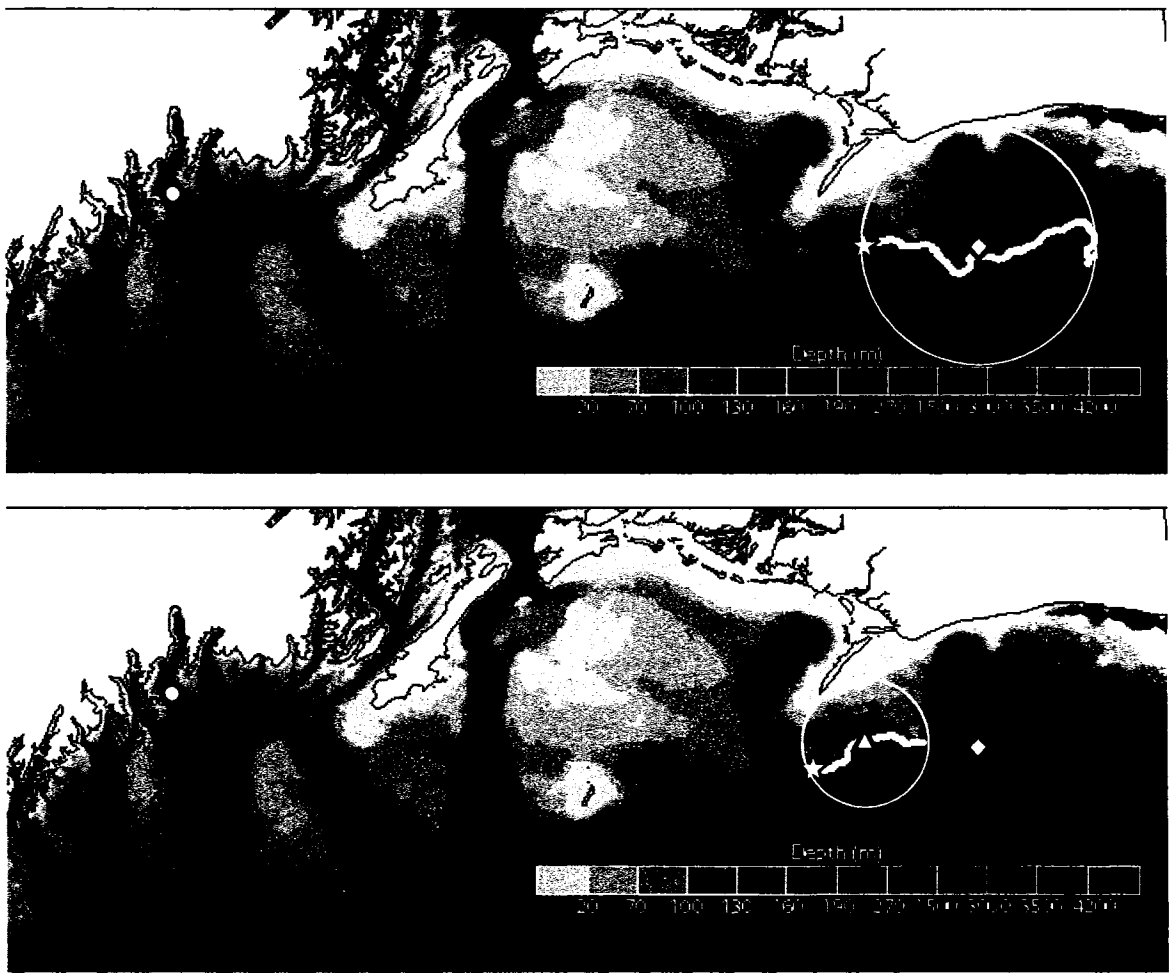

Fig. 3.2. The first two iterations in the minimum distance dispersal model for fish 00-0737b. The final location of the fish (◇) is used as the starting point of the model. The algorithm searches a specified radius (thin white circles) based on swimming speed (RATE in m/hr) and time since the last depth reading (ELAPSED H in hrs) for all locations (thick cyan line) that match the maximum depth (DEPTH in m) measured by the tag. The cyan isobath is the only place where max depth conforms to bathymetry. The solution to each iteration (☆) is the location that is closest to the tag and release location of the fish (O). The next iteration starts (Δ) at the solution to the previous iteration and iterations continue to be calculated until the fish reaches its tag and release location. To depict the movement of the fish from its release location to its final location, model results of locations are replayed as time progressing forward, i.e., reverse chronology from which it was calculated.

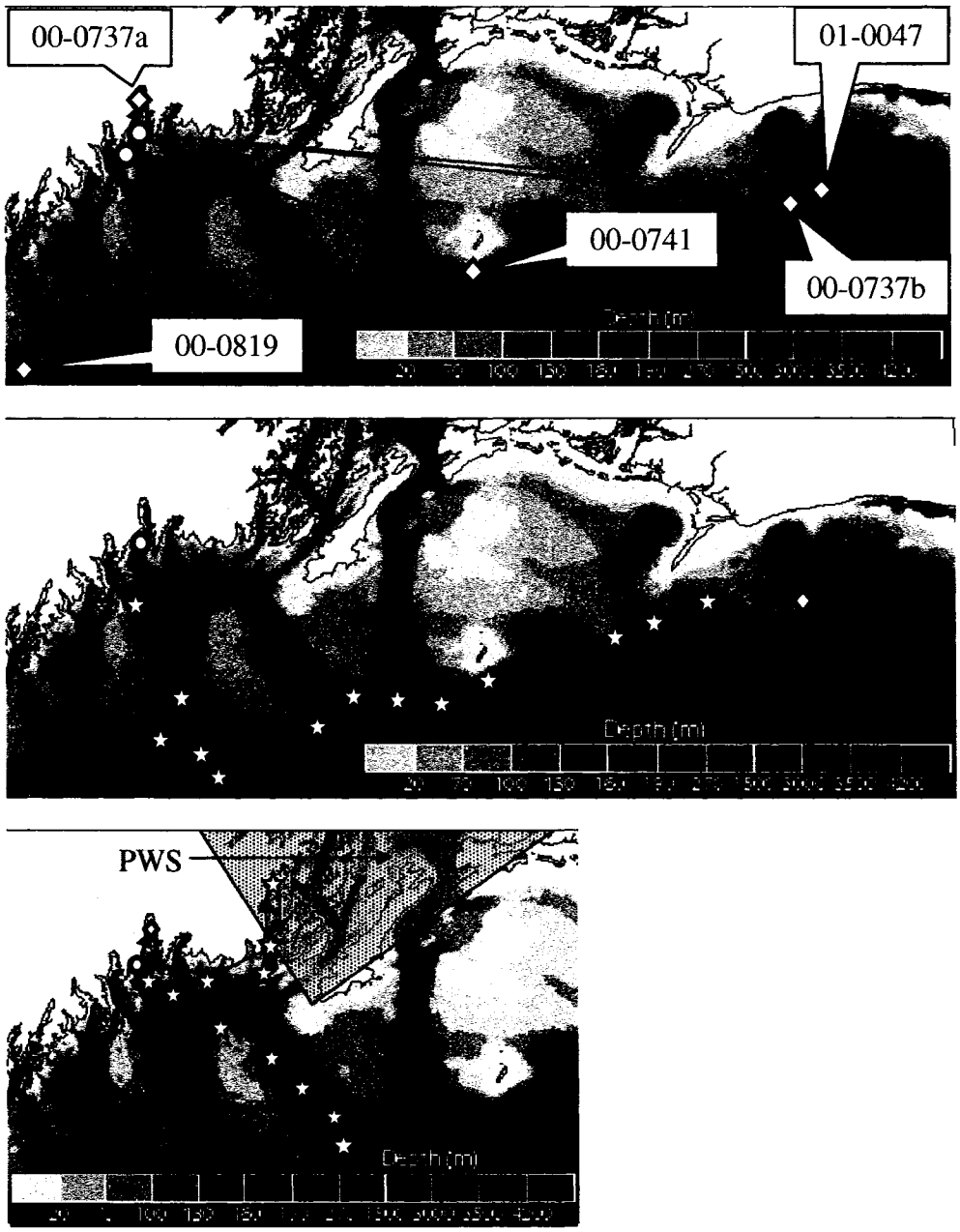

Fig. 3.3. Release and recovery locations and modeled dispersal paths. Upper panel - Release (◇) and recovery locations (O) for Pacific halibut in the Gulf of Alaska (from Seitz et al. 2003). Solid arrows indicate straightline paths. Middle panel - "One-way" dispersal path of fish 00-0737b (☆) determined by the minimum distance dispersal model. Lower panel - "Roundtrip" dispersal paths of fish 00-0737a (☆) determined by the minimum distance dispersal model. In the unrestricted scenario (solid line), the fish is able to access any location. In the restricted scenario (dashed line), the fish is unable to enter the shaded polygon area of Prince William Sound (PWS).

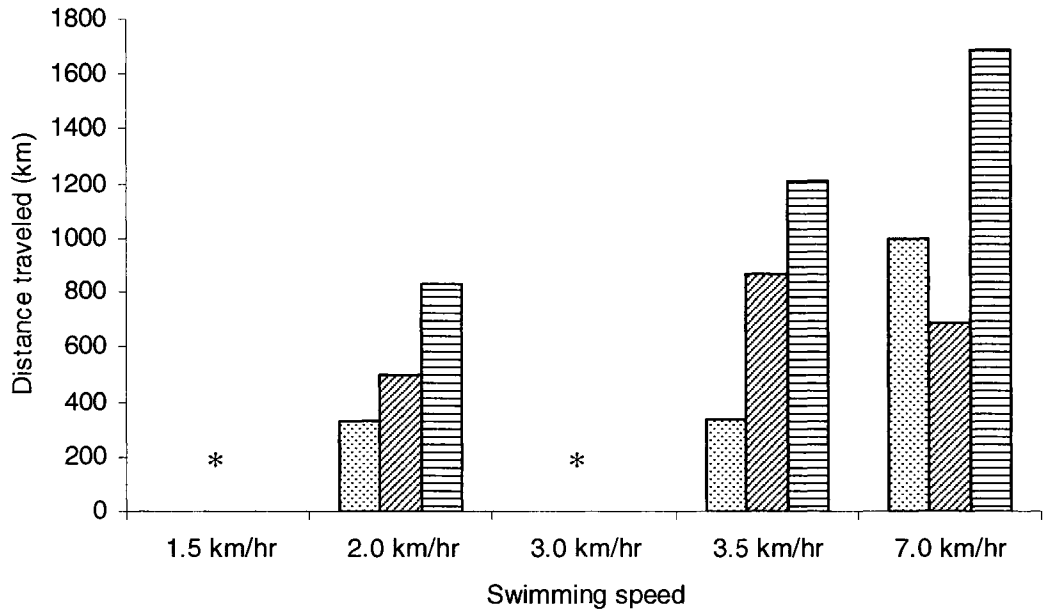

Fig. 3.4. Distance traveled estimated from different average swim speeds between early July and mid-November by fish 01-0047. * indicates speeds at which there was no bathymetric solution to the minimum distance model. Stippled areas = while on summer feeding grounds, diagonal lines = dispersal from summer grounds to winter grounds, and horizontal lines = total distance traveled.

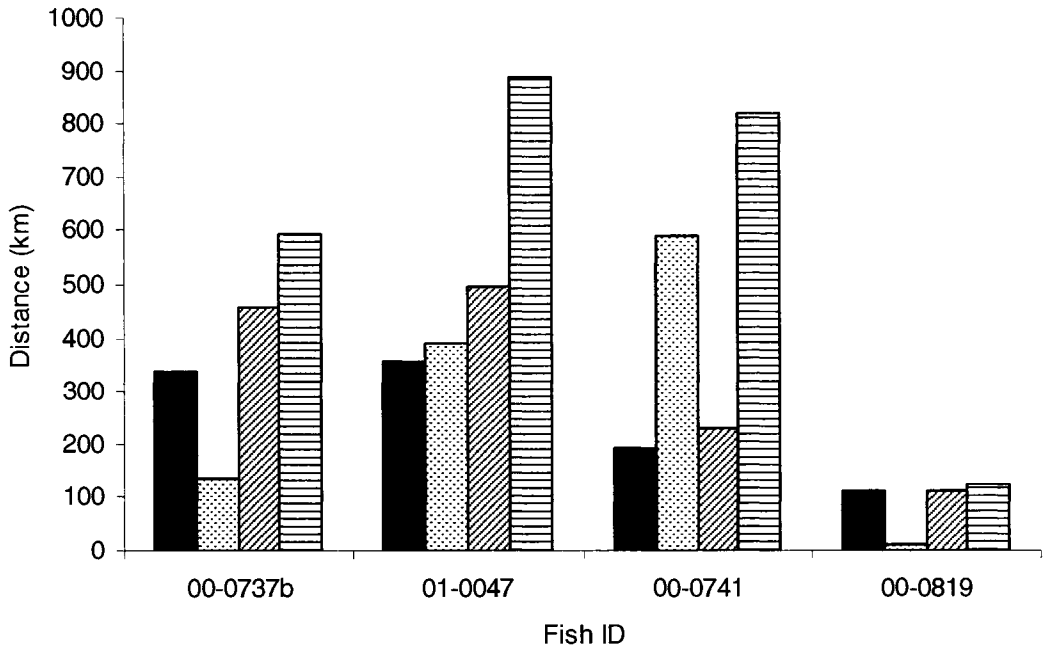

Fig. 3.5. Distance traveled by four fish that executed one-way dispersals at 2.0 km·hr^{-1}. Solid black areas = straight line distance between release and recovery locations, stippled areas = summer feeding grounds, diagonal lines = dispersal from summer grounds to winter grounds, and horizontal lines = total distance traveled.

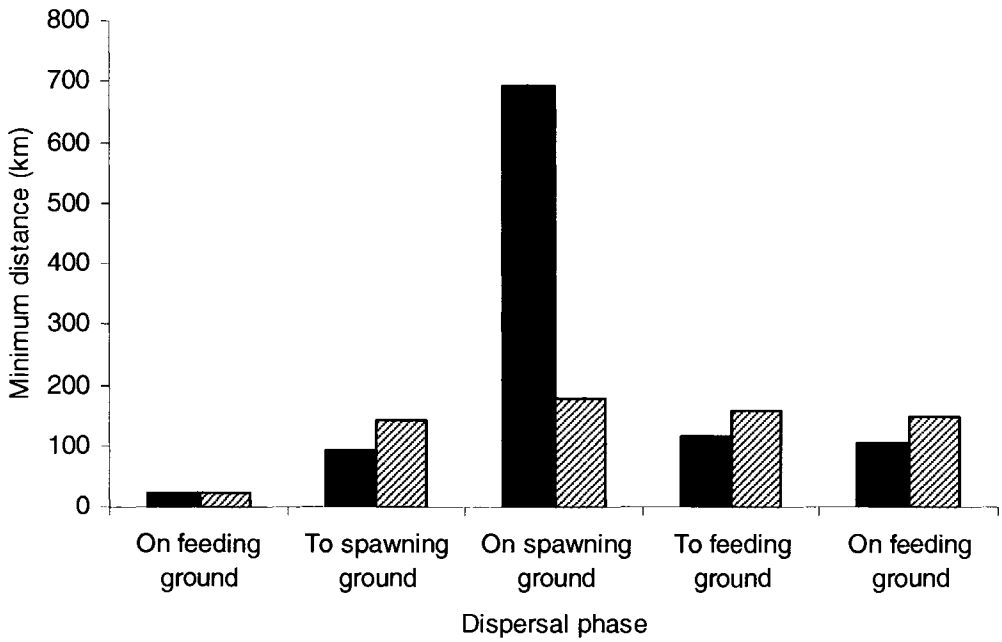

Fig. 3.6. Distance traveled by fish 00-0737a during different dispersal stages under unrestricted (solid bars) and restricted (lined bars) scenarios. Under the restricted scenario, the fish was not allowed to enter Prince William Sound.

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CHAPTER FOUR

Evidence of Pacific halibut *Hippoglossus stenolepis* population structure in the Bering Sea and Aleutian Islands[1]

ABSTRACT: Currently, Pacific halibut (*Hippoglossus stenolepis*) are managed as one population extending from California through the Bering Sea, but we hypothesize that Pacific halibut in the Bering Sea and Aleutian Islands belong to a separate population from those in the Gulf of Alaska. We studied the spawning locations and seasonal migration of Pacific halibut in the southeastern Bering Sea and Aleutian Islands as indicators of population structure. Pop-up Archival Transmitting tags provided no evidence that Pacific halibut moved out of the Bering Sea and Aleutian Islands region into the Gulf of Alaska during the mid-winter spawning season, supporting our hypothesis of separate populations. Within the Bering Sea and Aleutians region, there was evidence for geographically localized sub-populations as all of the Pacific halibut tagged near the Aleutian Islands displayed residency near the islands where they were tagged, with their movements possibly restricted by deep passes along the Aleutian Island chain. A spawning ground for a potential western Aleutians sub-population of Pacific halibut appears to be located to the east of Attu Island which is almost 1000 km to west of the nearest documented spawning area. In the southeastern Bering Sea, the Pacific halibut ranged farther from their tagging location than those from the Aleutian Islands.

[1] Seitz, A.C., T. Loher, B.L. Norcross, and J.L. Nielsen. In review. Evidence of Pacific halibut *Hippoglossus stenolepis* population structure in the Bering Sea and Aleutian Islands. Marine Ecology Progress Series.

Several fish moved among International Pacific Halibut Commission Regulatory Areas during the commercial fishing season, suggesting that the IPHC area boundaries may not accurately reflect the distribution of Pacific Halibut during the entire commercial fishing season.

INTRODUCTION

The Pacific halibut (*Hippoglossus stenolepis*) fishery is an important resource throughout western Alaska, with over nine million pounds (est. >$22 million ex-vessel) of product landed during 2005 in the southeast Bering Sea and Aleutian Islands (BSAI) directed fishery[2] (Fig. 4.1). About two million pounds were harvested by local communities under their Community Development Quotas[1] (CDQ). The CDQ program was first established by the North Pacific Fishery Management Council in 1992 to provide income to coastal communities with access to BSAI marine resources. The program has been hailed by the National Research Council as a critical innovation for local economic development (NRC 1999). Pacific halibut represent one of the keystone species within the program, thus its sound management on regional scales represents an important management objective within the context of the Magnuson-Stevens Fishery Management and Conservation Act.

Little is known about the ecology of Pacific halibut in the Bering Sea and along the Aleutian Islands. It is generally assumed that throughout their range in the entire

[2] http://www.fakr.noaa.gov/ram/ifqreports.htm (accessed 12 Jan. 2006)

northeast Pacific Ocean, adult Pacific halibut feed in shallow, nearshore areas during the summer, undertake a spawning migration to deeper water during winter and return to their summer grounds during spring (Dunlop et al. 1964, Best 1981). Spawning appears to be concentrated in relatively discrete winter spawning grounds near the edge of the continental shelf of the eastern Pacific, from at least British Columbia through the Pribilof Canyon (Fig. 4.1) in the southeast Bering Sea (St. Pierre 1984).

Currently, the International Pacific Halibut Commission (IPHC) does not manage BSAI Pacific halibut on a regional scale with separate population dynamics, but as part of a single, panmictic population of Pacific halibut in the entire eastern Pacific Ocean including the United States and Canada. This management paradigm was largely established due to four lines of evidence: (1) conventional tagging experiments (Skud 1977, review in Kaimmer 2000) in which a large portion of Pacific halibut tagged in the Bering Sea migrated to the Gulf of Alaska (GOA), (2) genetic studies that have not identified separate populations within the range of eastern Pacific halibut (Tsuyuki et al. 1969, Grant et al. 1984, Bentzen et al. 1999), (3) surveys that only identified major spawning grounds in the GOA and a small portion of the southeastern-most corner of the Bering Sea (St-Pierre 1984), and (4) a review of larval surveys in which it was concluded that southeast Bering Sea receives substantial larval input from GOA spawning stock (St-Pierre 1989).

Recently, it is recognized that several marine fish species have a more complex population structure than previously realized, and in many cases, management units contain population complexes with several spawning components (Stephenson 1999).

This may be the case with Pacific halibut because some of the evidence from which the single population paradigm was established is questionable. The vast majority of conventionally tagged fish have been juveniles that were released and recaptured during the feeding season from March to November when commercial fishing is allowed (IPHC 1998). To understand spawning population structure, it is necessary to determine where adults are located during the winter spawning season, the time when actual genetic exchange occurs. Additionally, the movement of juveniles from the Bering Sea to the GOA simply may be a contranatant migration to return to the location at which they were spawned. The previous genetic studies (Tsuyuki et al. 1969, Grant et al. 1984, Bentzen et al. 1999) have failed to sample the Bering Sea thoroughly and have used genetic markers that may have lacked the resolution required to identify populations. Finally, winter surveys have never been conducted along the Aleutian Islands or farther north than the Pribilof Canyon in the Bering Sea. Therefore, it is likely that previously unidentified spawning grounds occur along the Aleutian Islands and north of the Pribilof Canyon, and these may change our interpretation of population structure of Pacific halibut in the northeast Pacific Ocean.

We hypothesize that the BSAI region contains a separate spawning population of Pacific halibut in the eastern Pacific Ocean because this area is geographically separated from the GOA. The Aleutian Island chain forms a porous barrier between the GOA and the Bering Sea, and the Bering Sea gyre forms a potential retention area for eggs and larvae (Fig. 4.1; Stabeno et al. 1999). The combination of the barrier to adult movement and the possible retention gyre for eggs and larvae in the BSAI could limit the amount of

exchange with the GOA. Therefore, the goal of this study is to investigate Pacific halibut that feed during the summer in the Bering Sea and determine if they all remain there to spawn, or some move into the GOA. To accomplish this, we tagged adult Pacific halibut in the BSAI with Pop-up Archival Transmitting (PAT) tags. This technology allows us to determine winter location of the tagged fish and to infer migration timing and pathways used during their spawning migration without depending upon winter fisheries to recapture the tagged individuals.

MATERIALS AND METHODS

Wildlife Computers[3] PAT tags were externally attached to Pacific halibut following a previously successful protocol (Seitz et al. 2003). The fish were captured by commercial longline gear, pulled to the surface and brought onto the vessel in a net. The Pacific halibut were deemed appropriate for PAT tagging and release if they were at least 110 cm fork length (FL), as this was the smallest size of Pacific halibut successfully tagged in a previous study (Seitz et al. 2003), and they were likely to be sexually mature (Clark et al. 1999). The tags were connected to titanium darts with a tether that was 15 cm in length and constructed of 130 kg test monofilament fishing line wrapped in adhesive-lined shrink-wrap. The darts were inserted through the dorsal musculature and pterygiophores, anchoring them in the bony fin-ray supports of the fish. The position of

[3] Redmond, Washington, USA

the darts was about 2.5 cm medial of the fish's dorsal fin on the eyed-side of the fish where the body began to taper towards the tail.

Pacific halibut were tagged and released in three locations: St. Paul Island (n=12) during August 2002; Attu Island (n=13) and Atka Island (n=12) during July–August 2004 (Fig. 4.1). Thirty-four tags were programmed to release on 15 February the following year to determine the Pacific halibuts' winter grounds. The three remaining tags, all on fish captured and released near St. Paul, were programmed to release on 1 May 2003, to test site fidelity to summer feeding grounds.

Each PAT tag contained three electronic sensors that measured ambient water temperature, depth of the tag and ambient light (for PAT tag details, see Seitz et al. 2003). The PAT tags actively corroded the pin to which the tether was attached, thus releasing the tag from the animal. The tag then floated to the surface and transmitted summarized historical data records to the Argos satellite[4] system. Upon popping up, the tags' endpoint positions were determined from the Doppler shift of the transmitted radio frequencies in successive uplinks received during one Argos satellite pass (Keating 1995). The transmitted data then were processed further by Wildlife Computers' PC-based software.

The data were sampled at two minute intervals and were subsequently summarized into 12-hour periods by software within the PAT tag thus providing four types of data: 1. percentage of time spent within specific depth ranges; 2. percentage of time spent within specific temperature ranges; 3. depth-temperature profiles containing

[4] www.argosinc.com (accessed 12 Jan. 2006)

minimum and maximum depths and temperatures; and 4. ambient light levels during sunrise and sunset events. Light-based longitude estimates were produced by Wildlife Computers' proprietary software, Global Position Estimator (GPE), using the ambient light data (for details, see Seitz et al. in press). In short, GPE was used to identify daily sunrise and sunset events. Next, days with sunrise/sunset data that did not exhibit smoothly sloping light levels from high to low or low to high were rejected. Finally, GPE calculated longitude for the remaining days by comparing the local noon of the tag (mean of the sunrise and sunset times) to 1200 UTC (Coordinated Universal Time). Estimated longitude values that were outside the published range of the Pacific halibut, i.e., 140° E to 117° W (Mecklenburg et al. 2002), were rejected. Latitude estimates have been found to be highly variable in previous PAT tagging experiments and therefore were not used for determining movement of Pacific halibut (Seitz et al. in press).

RESULTS

Behavior

Based on pop-up locations and depth records, behavior of individual Pacific halibut were classified into four types (Fig. 4.2): (1) Shelf residents were fish that remained on the continental shelf for the duration of the experiment and never experienced depths greater than 200 m, (2) Slope migrators were Pacific halibut that were located on the continental slope in water deeper than 200 m on the pop-up date, (3) Long distance migrators were Pacific halibut that moved more than 200 km from their release

site and changed general areas, i.e., from the southeastern Bering Sea to the Aleutian Islands, and (4) Feeding-site returnees were fish whose pop-up locations were in close proximity to the location at which the fish were tagged and released. However, they could not have remained near their tagging locations for the duration of the experiment because they experienced maximum depths greater than 200 m. Depths of this magnitude do not exist on the continental shelf, indicating that the fish moved off the shelf to the slope during their time at-liberty. For all fish, large, abrupt changes in maximum depth were defined as the spawning migration from the continental shelf to the continental slope (Seitz et al. 2003).

Attu Island Pacific halibut

The fish ranged from 110 to 154 cm FL and were at-liberty for approximately 205 days (Appendix 4.1). Data were recovered from 11 of 13 tags (85%). All pop-up locations were within the group of islands where Attu Island is located, and the maximum horizontal displacement from the release site was 98.0 km while the minimum was 0.5 km (Fig. 4.3). The light-based longitudes did not demonstrate any large-scale east-west movements, thus the longitude records provided no evidence that the Pacific halibut departed the area during their time at-liberty (Appendix 4.2). Ambient water temperatures ranged from 3.2°C to 9.0°C in depths between 32 and 748 m (Appendices 4.1 and 4.2).

The Attu Island fish displayed three of the four general behaviors (Fig. 4.3, Appendix 4.2). Two fish were shelf residents and both moved in a southerly direction.

Seven fish were slope migrators and moved east-southeast. All of these fish were tagged in water less than 100 m depth. Spawning migrations occurred as early as 13 September and as late as 14 November. The remaining two Pacific halibut were feeding site returnees. These fish experienced maximum depths of approximately 400–600 m from early-December to late January, and subsequently moved back to their release locations.

Atka Island Pacific halibut

The tagged fish ranged from 111 to 147 cm FL and were at-liberty for approximately 195 days (Appendix 4.3). Data were recovered from only 5 of the 12 tags (42%). All pop-up locations were within the island group where Atka Island is located and the maximum horizontal displacement from the release site was 167 km while the minimum was 2 km (Fig. 4.3). Similar to the tags from Attu Island, the light-based longitudes did not demonstrate any large-scale east-west movements, thus the longitude records provided no evidence that the Pacific halibut departed the area during their time at-liberty (Appendix 4.4). The fish released near Atka Island experienced ambient water temperatures from 2.6°C to 8.0°C in depths between 84 and 712 m (Appendices 4.3 and 4.4).

The Atka Island fish displayed two of the four general behaviors (Fig. 4.3, Appendix 4.4). Two fish were slope migrators, but they behaved differently from each other with respect to timing of migration to deep water. One Pacific halibut left its tagging location immediately after release as evidenced by a gradual increase in depth until early October. At this time, the fish swam to the continental slope, where it

remained until the pop-up date. The other slope migrator remained at a depth consistent with its tagging location until early November at which time the fish moved to the continental slope. Three Pacific halibut were feeding site returnees as their PAT tags reported to Argos in close proximity to their respective release locations. These three fish all experienced maximum depths of greater than 400 m during the winter.

St. Paul Island Pacific halibut

Data were recovered from 9 of 12 tagged Pacific halibut, which ranged from 112 to 137 cm FL (Appendix 4.5). One fish was recaptured at its release location by a commercial longline vessel after only 12 days at-liberty. On 6 fish, the tags popped off and reported to Argos satellites after approximately 185 days at-liberty and on one fish, the tag reported after 258 days at-liberty. The last tag prematurely released from the fish after 42 days, drifted on the surface of the ocean for the next 142 days and then transmitted to the satellites on the scheduled date from above the Shirshov Ridge in Russian waters (Fig. 4.3).

The St. Paul Island Pacific halibut had a broader range of horizontal displacements than fish released near Attu and Atka Islands (Fig. 4.3; Appendix 4.5). For fish whose tags remained attached, the maximum horizontal displacement from the release site was 513 km while the minimum was 0 km. The fish released near St. Paul Island experienced ambient water temperatures from 1.4°C to 9.4°C in depths between 12 and 844 m (Appendices 4.5 and 4.6).

For all but one fish, every light-based longitude was west of Unimak Pass (164.9° W; Appendix 4.6), the easternmost connection between the Bering Sea and Gulf of Alaska. Therefore, there is no evidence that any of these Pacific halibut may have spent time in the Gulf of Alaska and returned to the Bering Sea during their time at-liberty. For one fish, there were 2 of 27 longitude estimates east of 164.9° W (Appendix 4.6). However, there was considerable variability among consecutive longitude estimates (Appendix 4.6) and the fish's pop-up location was close to its release location. As there was no trend in longitude estimates to the east, the fish most likely remained in the Bering Sea.

The St. Paul Island fish displayed all of the four general behavior types (Fig. 4.3; Appendix 4.6). Two fish were shelf residents; both swam to the west, but remained in depths between 40 and 92 m for the duration of the experiment. Three fish were slope migrators and all experienced depths greater than 650 m. The time at which the fish moved to the continental slope varied from late November to mid-January. One fish displayed movement on a larger scale and swam to Yunaska Island in the eastern Aleutian Islands (513 km; Fig. 4.3). The longitude estimates showed a trend of movement away from the tagging area towards the east, beginning in September. Once the fish reached approximately 166° W longitude, the tag stopped producing longitude estimates, which coincided with the fish moving into deeper water (Fig. 4.2, lower right panel). The last fish had the only tag that reported in May 2003, and this Pacific halibut was a feeding site returnee. This fish moved to the slope in late-December and returned

to the shelf at the end of February. The behavior of two fish could not be elucidated: the fish captured shortly after tagging, and the fish that experienced premature tag release.

DISCUSSION

Adult spawning locations and movement patterns should affect the population structure of Pacific halibut in the Bering Sea and the GOA. If adults from a common feeding area disperse to numerous spawning areas and mingle with fish from several other feeding areas, then the population will be reproductively mixed. In contrast, if adults from a common feeding area display directed movements to a discrete spawning area and do not reproductively mix with fish from other feeding areas, then the population structure may be more complex than is currently recognized (Stephenson 1999).

The results of this study are consistent with the hypothesis that BSAI Pacific halibut may constitute a separate spawning population from those in the GOA. There was no evidence that any fish tagged on summer feeding grounds in the BSAI migrated to the GOA in the winter spawning season. If all of the adult Pacific halibut remain in the Bering Sea to spawn, their eggs and larvae will likely become entrapped in the Bering Sea gyre or one of the smaller sub-gyres within the Bering Sea (Stabeno et al. 1999). If this pattern is continued for many generations, in the absence of juvenile emigration and if individuals that were advected from the GOA into the Bering Sea as larvae return to the

Gulf as adults, Bering Sea Pacific halibut should be reproductively isolated from those in the GOA.

To complement this study, Pacific halibut have also been PAT tagged in the GOA during the summer with winter pop-up dates (Seitz et al. 2003, Loher and Seitz 2006). The fish tagged in the southeast and southwest GOA demonstrated a northward migration towards major spawning grounds in the GOA, but not to the BSAI region. None of those Pacific halibut moved into the BSAI from the GOA, further supporting our hypothesis that the Bering Sea contains a local, resident population of Pacific halibut separate from that in the GOA.

All of the Pacific halibut tagged near Attu and Atka Islands appear to have remained in the vicinity of the island near which they were released, and did not cross any passes along the Aleutian Island chain. The Pacific halibut released near Attu Island did not cross Near Strait (depth = 2000 m) to the west and Buldir Strait (depth = 640 m) to the east (Fig. 4.3). The Pacific halibut released near Atka Island did not cross Amchitka Pass (depth = 1155 m) to the west and Amukta Pass (depth = 430 m) to the east (Fig. 4.3). The long distance migrator tagged near St. Paul Island swam to the eastern side of Amukta Pass, but like the Pacific halibut tagged near Atka, did not cross the pass. Only the depths of Amchitka Pass and Near Straight exceed the maximum depth recorded by a Pacific halibut (844 m), but the fish in this study apparently did not cross shallower passes either. Because Pacific halibut are found in depths greater than those of both Buldir Strait and Amukta Pass, the depth of the pass *per se* does not appear to be the barrier to movement, but rather other factors such as swift currents and strong

turbulence found in many Aleutian passes may limit movement (Hunt and Stabeno 2005). If Aleutian passes indeed restrict movement of Pacific halibut, sub-populations belonging to a larger BSAI population may exist along the Aleutian Islands.

The final locations of the Pacific halibut imply that the documented range of spawning areas (St-Pierre 1984) may be incomplete. In this study, we assume that the Pacific halibut on the slope are at their winter spawning locations because virtually all Pacific halibut in the size range of this study are mature (Clark et al. 1999). Peak spawning is expected during late-January and February (Thompson and Van Cleve 1936), thus the mid February pop-up date maximizes the likelihood that tagged fish will be located on their spawning grounds. The fish that swam to the continental slope northwest of the Pribilof Canyon suggests that spawning grounds may extend along the shelf-edge north of the Pribilof Canyon, but we are unable to ascertain this because there have been no spawning surveys north of the canyon (St-Pierre 1984).

Along the Aleutians, a major Pacific halibut spawning ground of a possible western Aleutians sub-population appears to be located to the east of Attu Island where several of the fish were located at the end of the study. If this is indeed a major spawning ground, it is the first one reported along the Aleutian Island chain, and it is almost 1000 km to west of the nearest known spawning area. In contrast, the Pacific halibut tagged near Atka Island did not move to a single discrete area and hence there was no evidence to identify the location of a potential major spawning ground in the area. However, this conclusion may be confounded by the small sample size of tags from Atka Island and needs to be tested further.

Several of the Pacific halibut displayed feeding site fidelity. The frequent occurrence of summer feeding site fidelity in this study and a previous study (Seitz et al. 2003) demonstrates that a large proportion of adults may return to the same area annually, making them vulnerable to local depletions in areas with intensive commercial fisheries. St. Paul Island is an example where harvest shortfalls over the last five years have been 14–56% of the annual catch limits, suggesting sensitivity of the Pacific halibut population to locally concentrated exploitation that eventually results in local depletion (Hare and Clark 2004). This indicates that the movement of individual Pacific halibut may be relatively limited in the Bering Sea, in contrast to the complete mixing assumed by the present management scenario that does not recognize biological independence among individual Bering Sea Regulatory Areas.

There are several possible explanations for shelf residency of Pacific halibut in the BSAI. The fish may have foregone a trip to the continental slope and spawned on the continental shelf (St-Pierre 1984, IPHC 1998). It is also possible that the shelf residents would have spawned later in the year and a February pop-up date was too early to capture the spawning migration. Alternatively, these Pacific halibut may be non-annual spawners (Novikov 1964, Seitz et al. 2005). Recently, it has been recognized that several iteroparous fish species may be non-annual spawners (Rideout et al. 2005). The percentage of non-reproductive fish must be determined if stock-recruitment models are to accurately portray spawning numbers or biomass, and PAT tags may be one method to generate hypotheses regarding potential skip-spawning rates based on year-round shallow water residence. For Pacific halibut, skipped spawning rates do not present a major

management issue because recruitment forecasts are based more on environmental forcing than on a stock-recruitment relationship, *per se*. However, if skipped spawning is a common feature within the population and varies according to condition index or environmental parameters, effective population size may vary even if total abundance remains static.

The Pacific halibut that swam from St. Paul Island to the Aleutian Islands illustrates that in some cases, Pacific halibut may swim much farther than the straight-line distance between the tagging and pop-up locations. This fish could have taken various routes from the beginning to the end of its time at-liberty. One possibility is that it swam straight from the tagging location to the pop-up location across the Bering Basin, leaving the bottom and maintaining a depth of 400–800 m. Alternatively, it may have swum circuitously southeast then southwest following the continental slope between approximately 400 and 800 m to arrive at its final location. The light-based longitude record demonstrates that the fish swam to the east and reached approximately 165° W longitude before moving westward to its final destination. This circuitous migration route increases the distance traveled from a straight-line distance of 513 km to approximately 775 km. If Pacific halibut routinely migrate near the bottom rather than across ocean basins, migration distances of several Pacific halibut in a previous study (Loher and Seitz 2006) are actually greater.

Several Pacific halibut tagged near St. Paul Island moved among IPHC Regulatory Areas. The history of IPHC Regulatory Areas within the Bering Sea is relatively complex. Initially, the Bering Sea was managed as a single unit (IPHC 1962),

but in 1966 was subdivided into numerous smaller units (IPHC 1967). A separate Regulatory Area encompassing the Pribilof Islands (IPHC Regulatory Area 4C; Fig. 4.3) was created in 1986 (Sadorus and St. Pierre 1995), primarily to provide economic benefits to St. Paul and St. George Islands following the termination of commercial fur seal (*Callorhinus ursinus*) harvests. The depth records indicate all but one tagged Pacific halibut in this study exceeded the maximum depth found in Regulatory Area 4C (145 m) and therefore left the Area at some time over the winter. Two of these fish left before the close of the fishing season in mid-November. Apparently, the current Regulatory Area does not encompass all habitats used throughout the year by those Pacific halibut that feed near the Pribilof Islands during the summer. Interception of fish that have left Area 4C for the spawning grounds before the end of the commercial fishing season may add to the local depletion observed in Regulatory Area 4C. In order to represent a region that is biologically meaningful to the Pribilof Islands during the entire commercial fishing season, Area 4C would need to be enlarged to more accurately reflect seasonal redistribution of Pacific halibut.

In contrast to fish near St. Paul, none of the fish tagged near Attu and Atka Islands, emigrated from IPHC Regulatory Area 4B (Fig. 4.3). IPHC Regulatory Area 4B apparently encompasses the boundaries of a possible sub-population(s) of Pacific halibut identified in this study.

We experienced two problems typical to PAT tagging experiments: premature release and non-reporting. The tag that released before the scheduled pop-up date was the first documented case of premature release in Pacific halibut PAT tagging

experiments, out of a total of 65 tags from this and previous studies (Seitz et al. 2003, Loher and Seitz 2006). This rate of premature release is well below those for other pelagic fish experiments (Domeier et al. 2003, Stokesbury et al. 2004). We speculate that PAT tags on Pacific halibut tend to experience fewer premature release events than those on pelagic fish because Pacific halibut live a more sedentary life and swim at slower speeds than highly migratory pelagic fish. Another problem that potentially affected our conclusions was the discrepancy in reporting rates between the tags released near Attu and St. Paul Islands, and those released near Atka Island. The Attu Island tags had the highest reporting rate of any Pacific halibut satellite tagging experiment, while the Atka Island tags had the lowest (Seitz et al. 2003, Loher and Seitz 2006). Considering that all of the tags were deployed by the same scientist under similar conditions, we suspect that a portion of the Atka Island batch of tags had faulty batteries. This claim is evidenced by a Pacific halibut that was recaptured more than a year later near its release site with the tag still attached. This tag was diagnosed by its manufacturer as having a dead battery.

Pacific halibut are a broadly distributed marine fish species in the North Pacific Ocean whose population appears to be potentially structured. The behavior of Pacific halibut in this study is consistent with the hypothesis that the BSAI region supports a local, resident population, with possible smaller sub-populations in the central and western Aleutians. If there is a separate population of Pacific halibut in the BSAI, its dynamics may vary from those of the GOA and determining its population dynamics will be necessary for correct modeling to predict how different populations will respond to future fishing pressure and changes in environmental conditions. Sample sizes in the

present study are insufficient to quantitatively address these questions, but this study provides qualitative information that can be used to direct future research.

Acknowledgments. This project was made possible by: Capt. S. Swetzof Jr. and crew of the F/V *Wind Dancer*, Capt. R. Zwahlen and crew of the F/V *Heritage*, and Capt. J. Martindale and crew of the F/V *Pacific Sun* during fishing operations; International Pacific Halibut Commission Port Sampler L. O'Neil for St. Paul Island logistics; P. Lestenkof of Central Bering Sea Fishermen's Association for housing on St. Paul Island; IPHC Sea Samplers R. Ames, E. Ekroth, L. Mattes and A. Williams for tagging assistance. Partial funding for this project was provided by the Exxon Valdez Oil Spill Trustee Council, the International Pacific Halibut Commission, the U.S. Geological Survey–Alaska Science Center and the University of Alaska Fairbanks School of Fisheries and Ocean Sciences. The findings presented by the authors are their own and not necessarily the position of the EVOS Trustee Council.

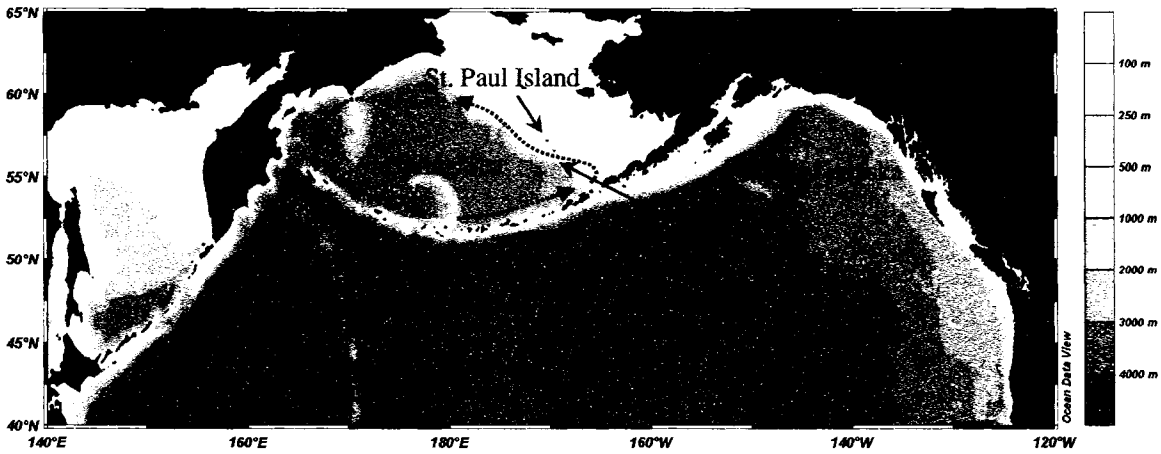

Figure 4.1. Map of North Pacific Ocean. Dotted lines indicate the dominant circulation pattern in the Bering Sea (Stabeno et al. 1999).

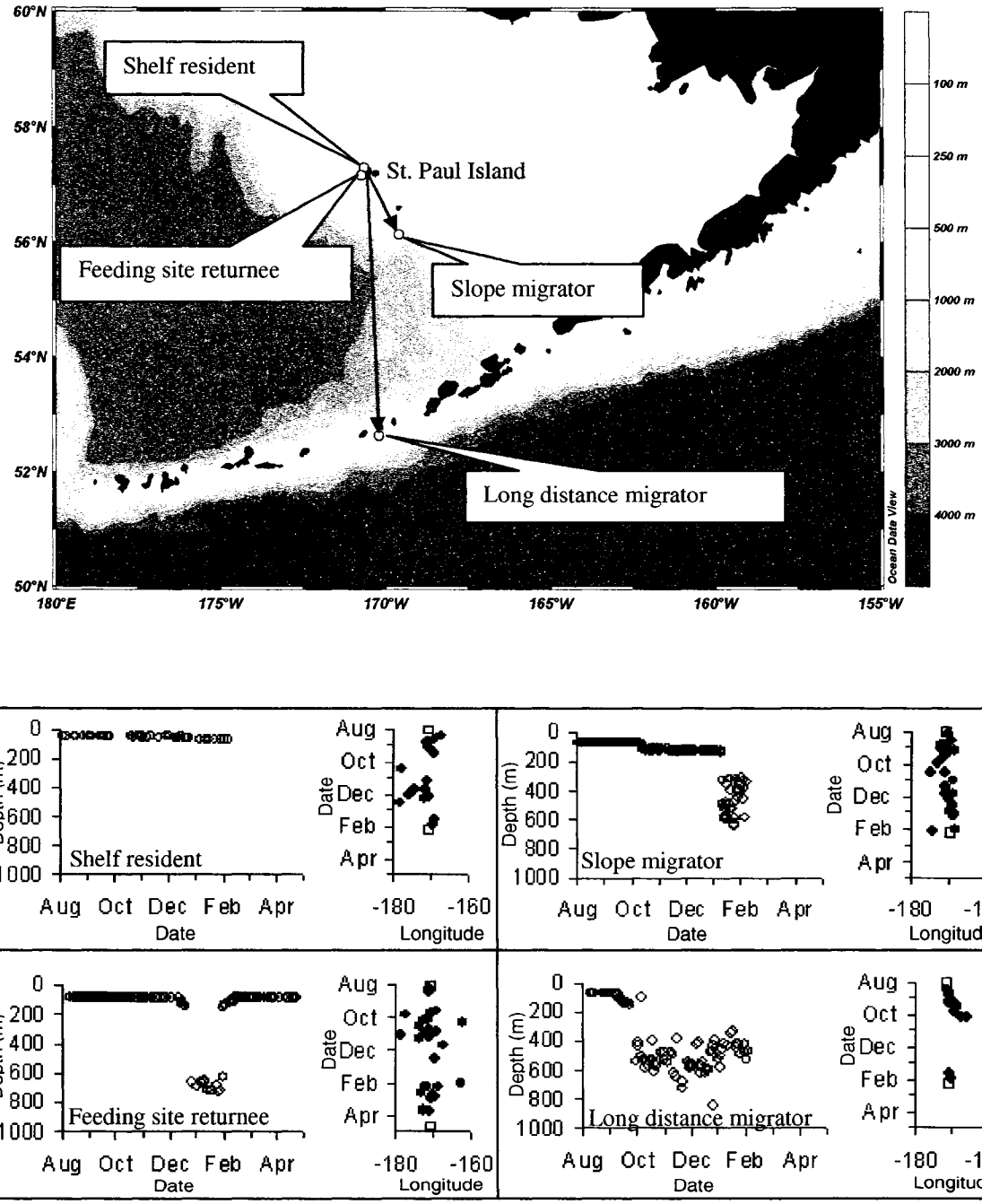

Figure 4.2. Examples of the four general behavior types of Pacific halibut. For depth plots, o = Maximum depth for 12-hour summary periods. For longitude plots, □ = release position and location at which the tag reported to Argos and ● = estimated position.

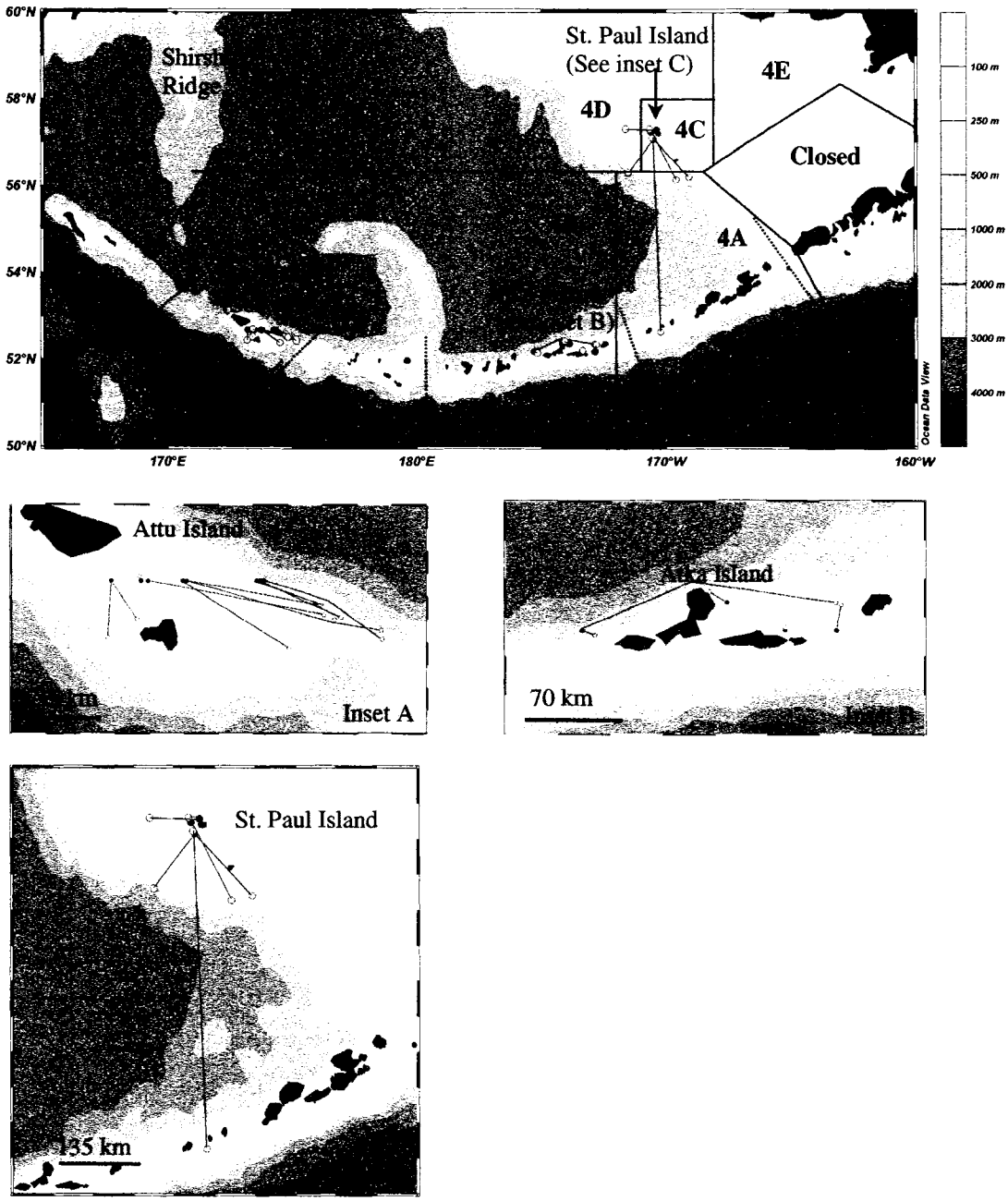

Figure 4.3. Release (●) and recovery sites (o) of PAT-tagged Pacific halibut in the Bering Sea and Aleutian Islands. Solid lines delineate International Pacific Halibut Commission Regulatory Areas and boldface type denotes Regulatory Area names. Dotted lines indicate passes between the Aleutian Islands.

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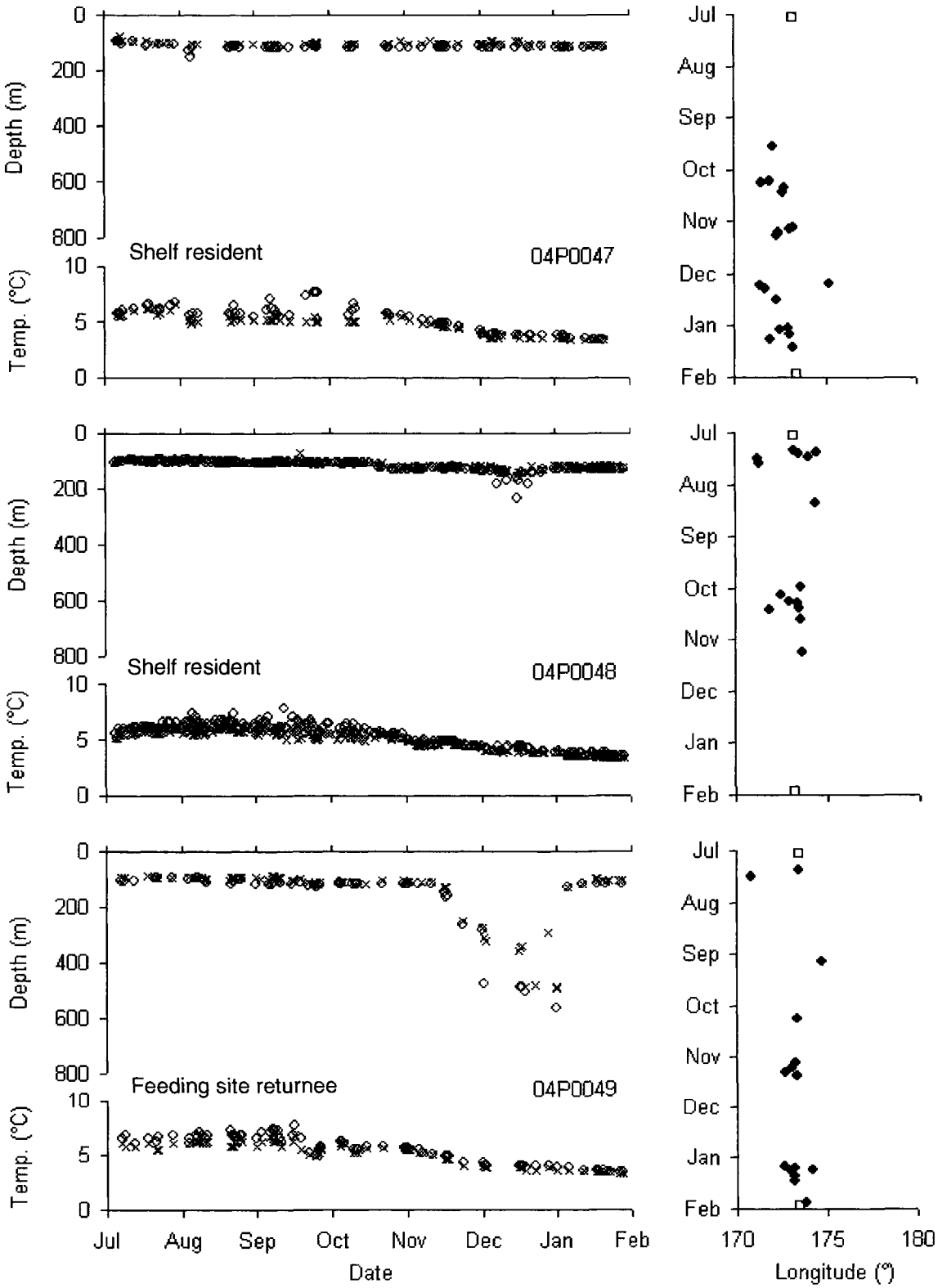
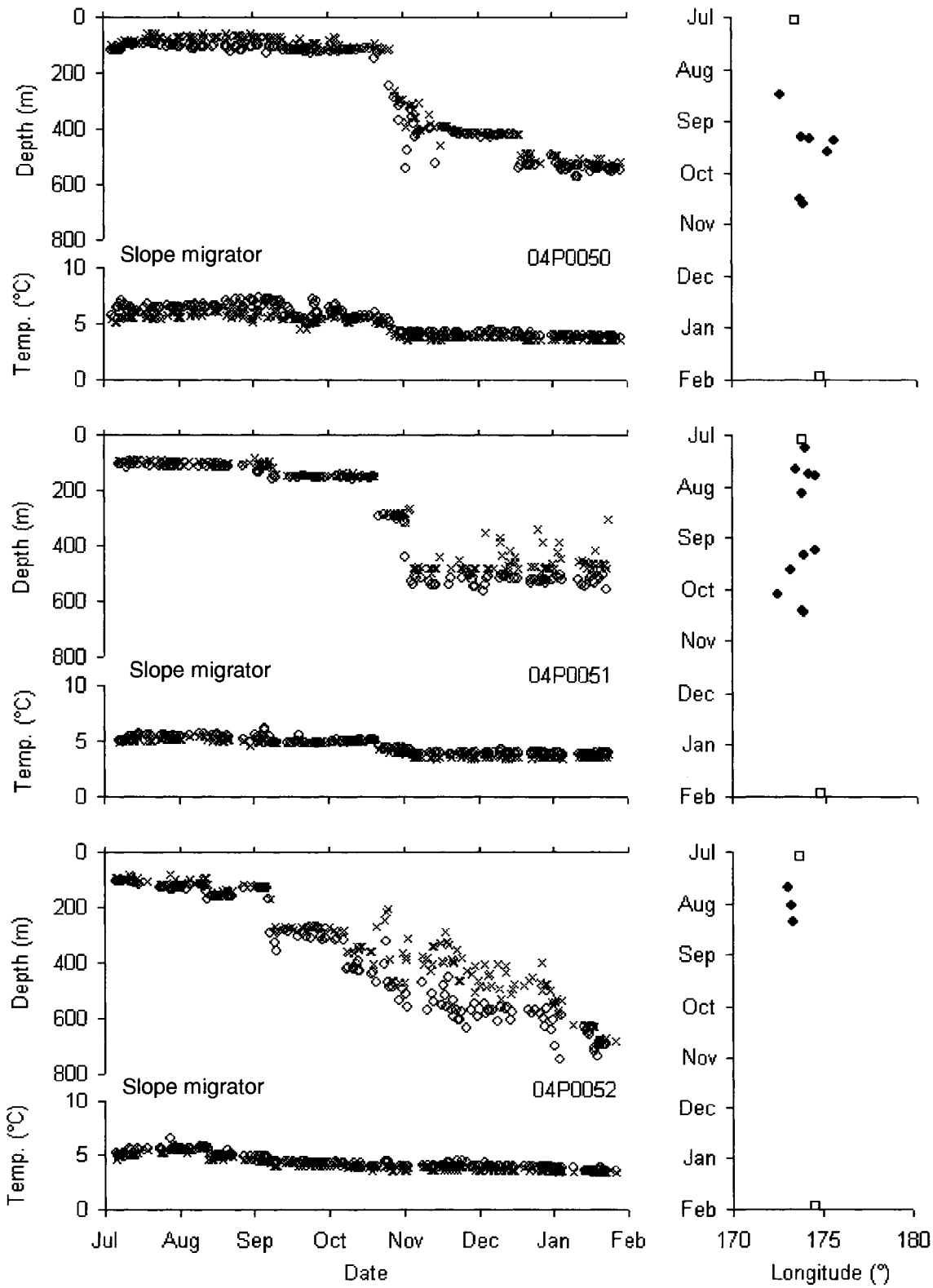
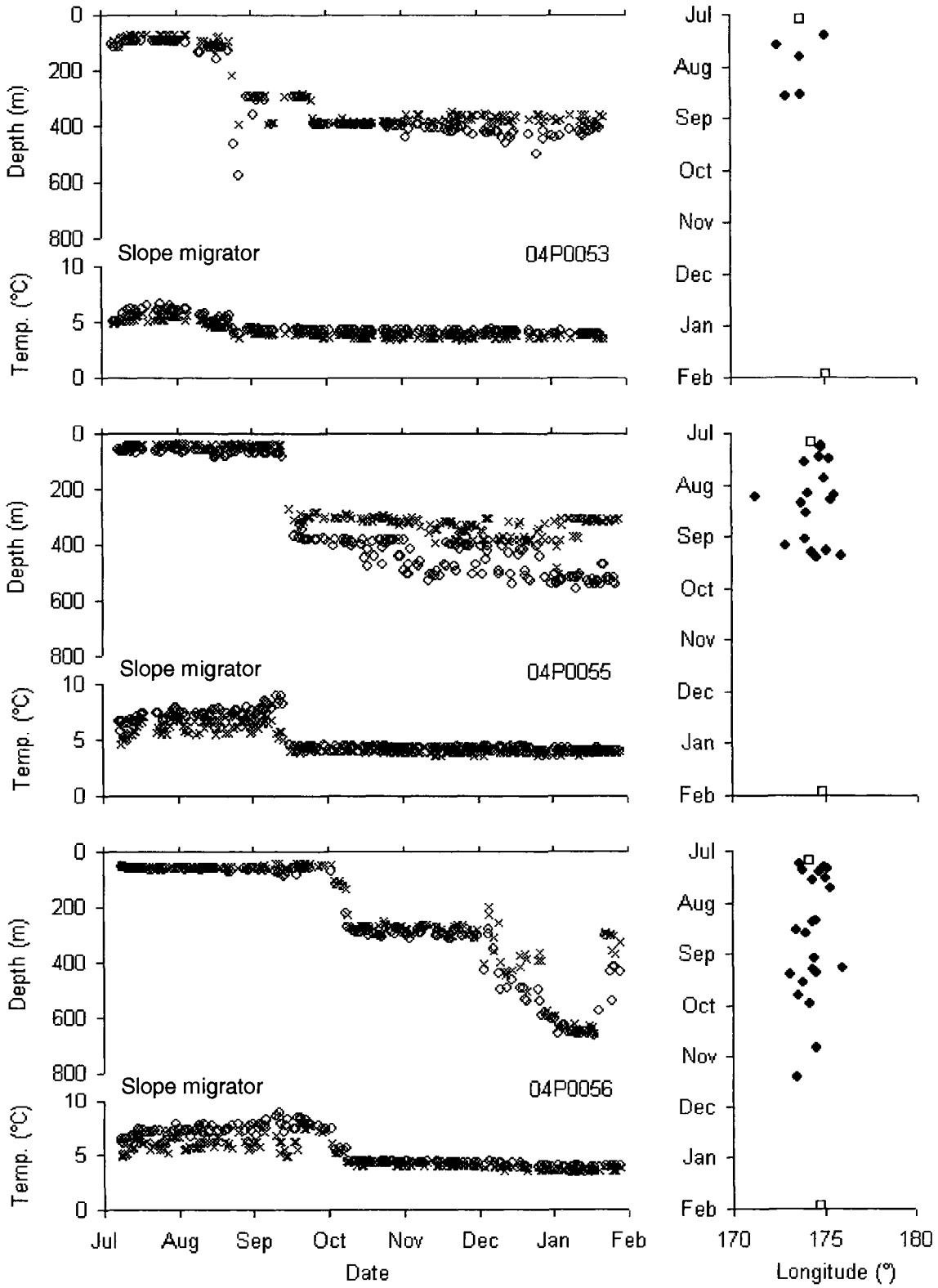
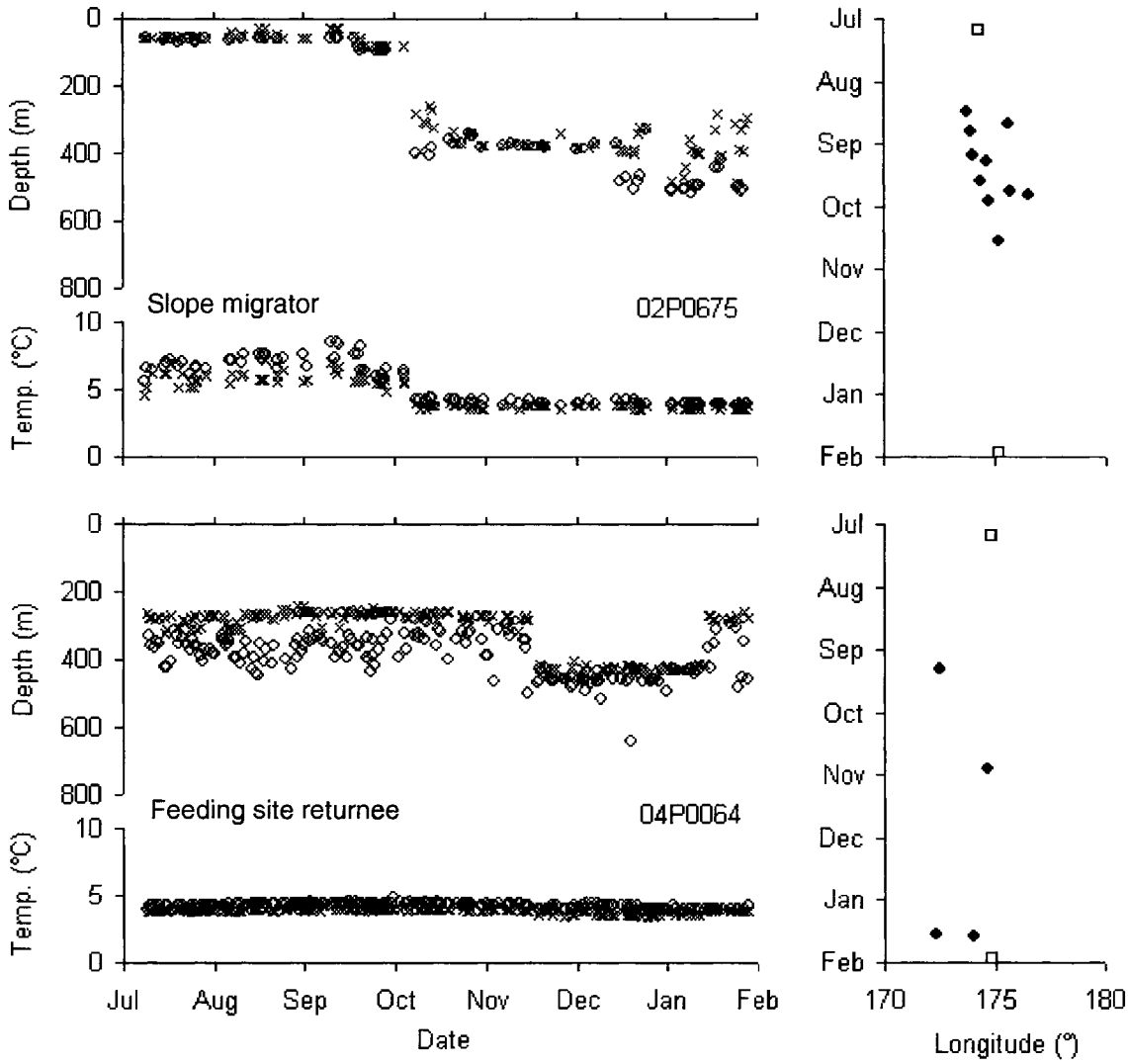
Appendix 4.1. Deployment summary for Pacific halibut near Attu Island. The fish were tagged and released between 24 July and 28 July 2004 and the tags popped up on 15 February 2005. Tag numbers correspond to those shown in Appendix 4.2. Longitude analysis is discussed fully in Seitz et al. (in press).

Tag #	04P0047	04P0048	04P0049	04P0050	04P0051	04P0052	04P0053	04P0055	04P0056	02P0675	04P0064
Length (cm)	110	154	135	146	111	112	115	144	144	129	142
Horizontal displacement (km)	22.3	27.3	2.1	87.6	67.1	61.3	98.0	43.3	33.3	64.4	0.5
Minimum depth (m)	76	72	88	56	84	84	68	36	40	32	240
Maximum depth (m)	152	236	564	568	564	748	576	556	664	520	644
Minimum temp. (°C)	3.4	3.4	3.2	3.6	3.4	3.4	3.4	3.6	3.4	3.6	3.4
Maximum temp. (°C)	7.6	7.8	7.6	7.4	6.2	6.4	6.6	9.0	8.8	8.6	4.8
Days with longitude	19	15	15	7	11	3	5	18	22	10	4
% of days with longitude	9.2	7.3	7.3	3.4	5.4	1.5	2.4	8.9	10.9	5.0	2.0
# of comparison days	0	1	0	0	1	0	0	2	5	0	0
Long. error magnitude (° ± SD)	NA	0.0	NA	NA	0.2	NA	NA	0.6	0.6	NA	NA
Long. bias (° ± SD)	NA	0.0	NA	NA	-0.2	NA	NA	-0.6	-0.2	NA	NA





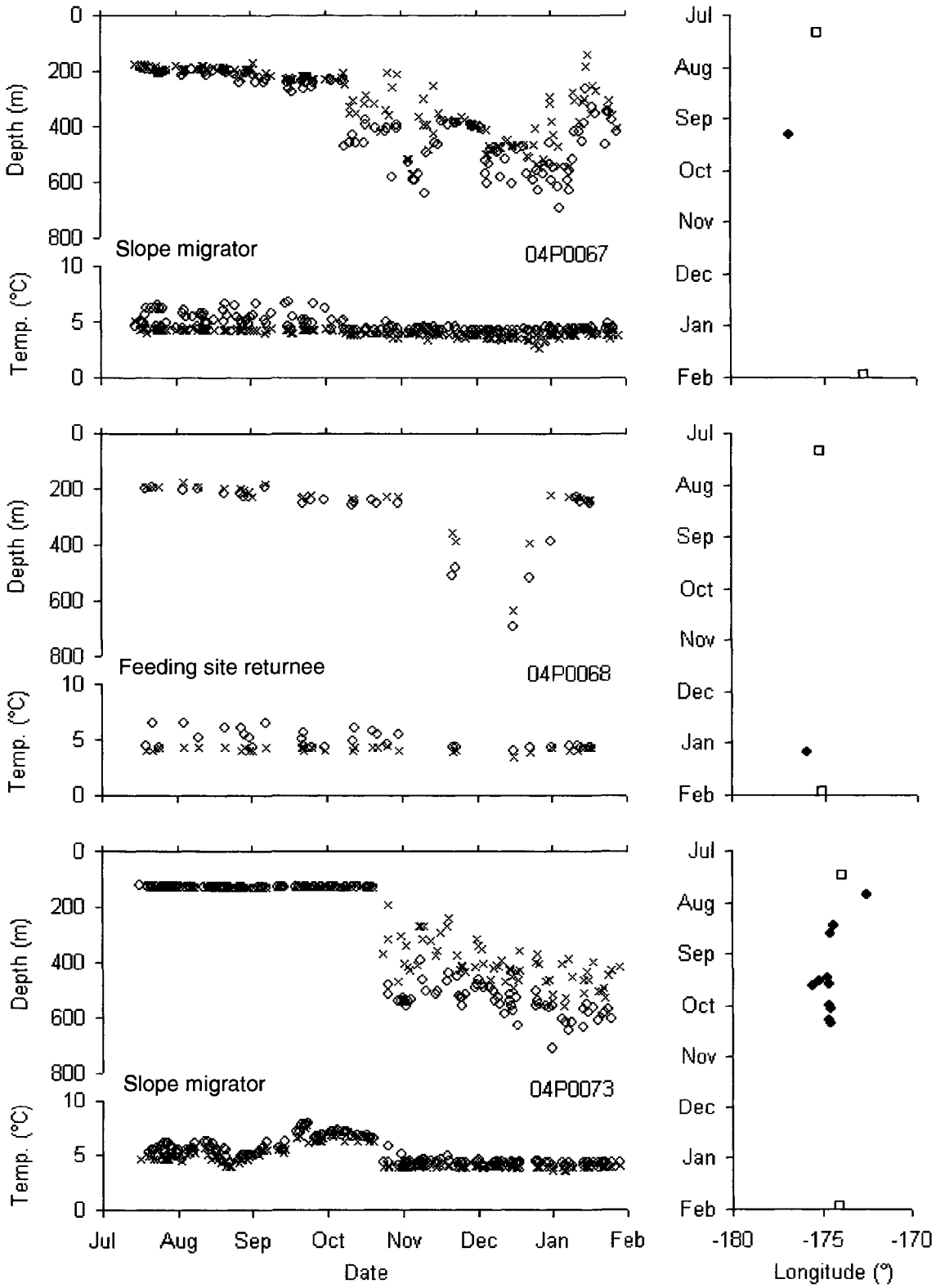


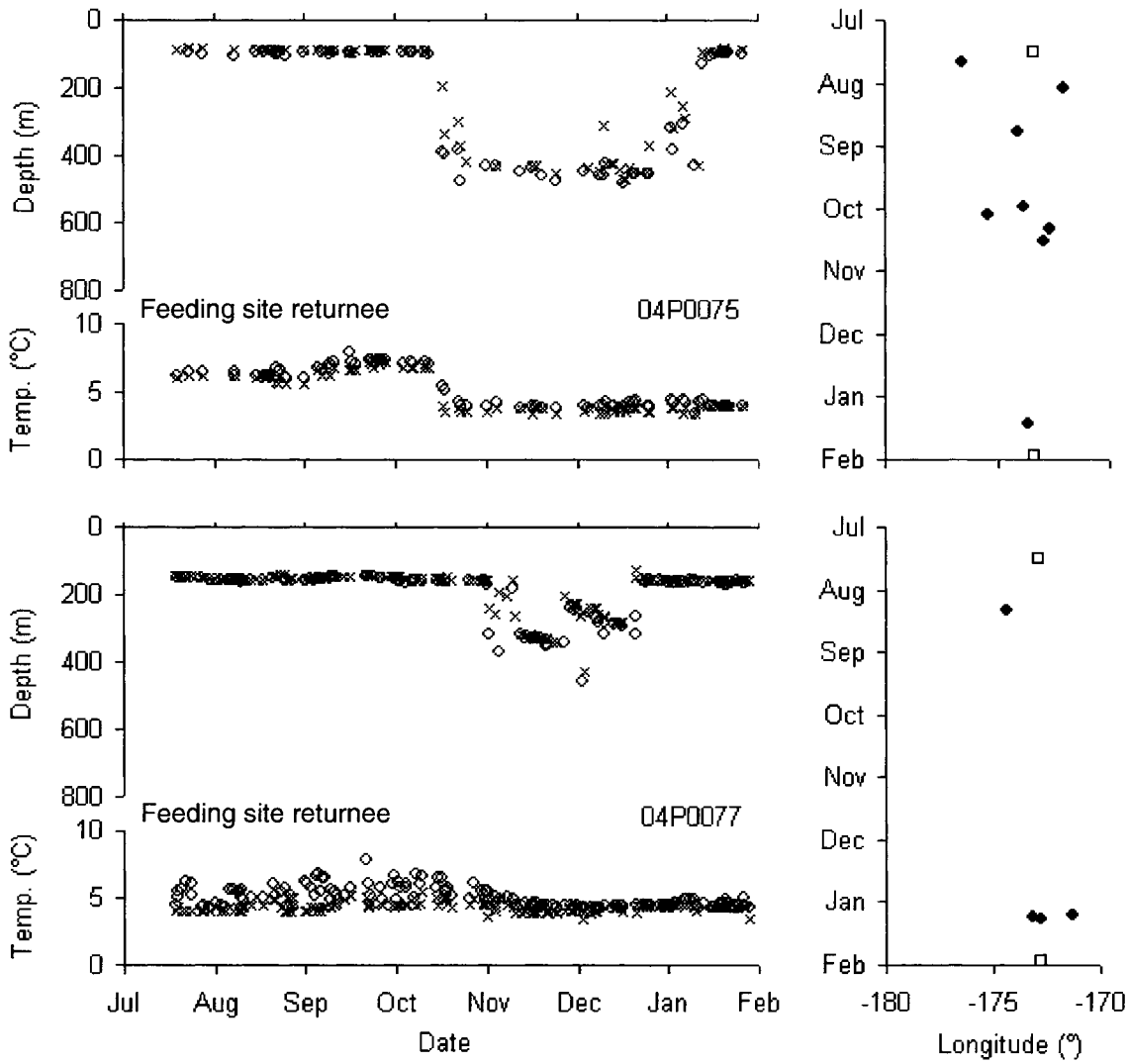


Appendix 4.2. Depth, temperature and longitude of Attu Island Pacific halibut. Maximum (o) and minimum (x) depths and temperatures are shown for each 12-hour summary period, as well as daily longitude estimates after outliers were removed. For longitude plots, □ = release position and location at which the tag reported to Argos and ● = estimated position. Tag numbers correspond to those shown in Appendix 4.1.

Appendix 4.3. Deployment summary for Pacific halibut near Atka Island. The fish were tagged and released between 1 August and 6 August 2004, and the tags popped up on 15 February 2005. Tag numbers correspond to those shown in Appendix 4.4. Longitude analysis is discussed fully in Seitz et al. (in press).

Tag #	04P0067	04P0068	04P0073	04P0075	04P0077
Length (cm)	111	147	128	117	127
Horizontal displacement (km)	166.6	7.6	13.5	1.8	18.2
Minimum depth (m)	144	176	124	84	132
Maximum depth (m)	696	692	712	480	460
Minimum temp. (°C)	2.6	3.4	3.6	3.4	3.4
Maximum temp. (°C)	6.8	6.4	7.8	8.0	7.8
Days with longitude	1	1	11	8	4
% of days with longitude	0.5	0.5	5.7	4.1	2.1
# of comparison days	0	0	0	1	0
Long. error magnitude (° ± SD)	NA	NA	NA	3.2	NA
Long. bias (° ± SD)	NA	NA	NA	-3.2	NA

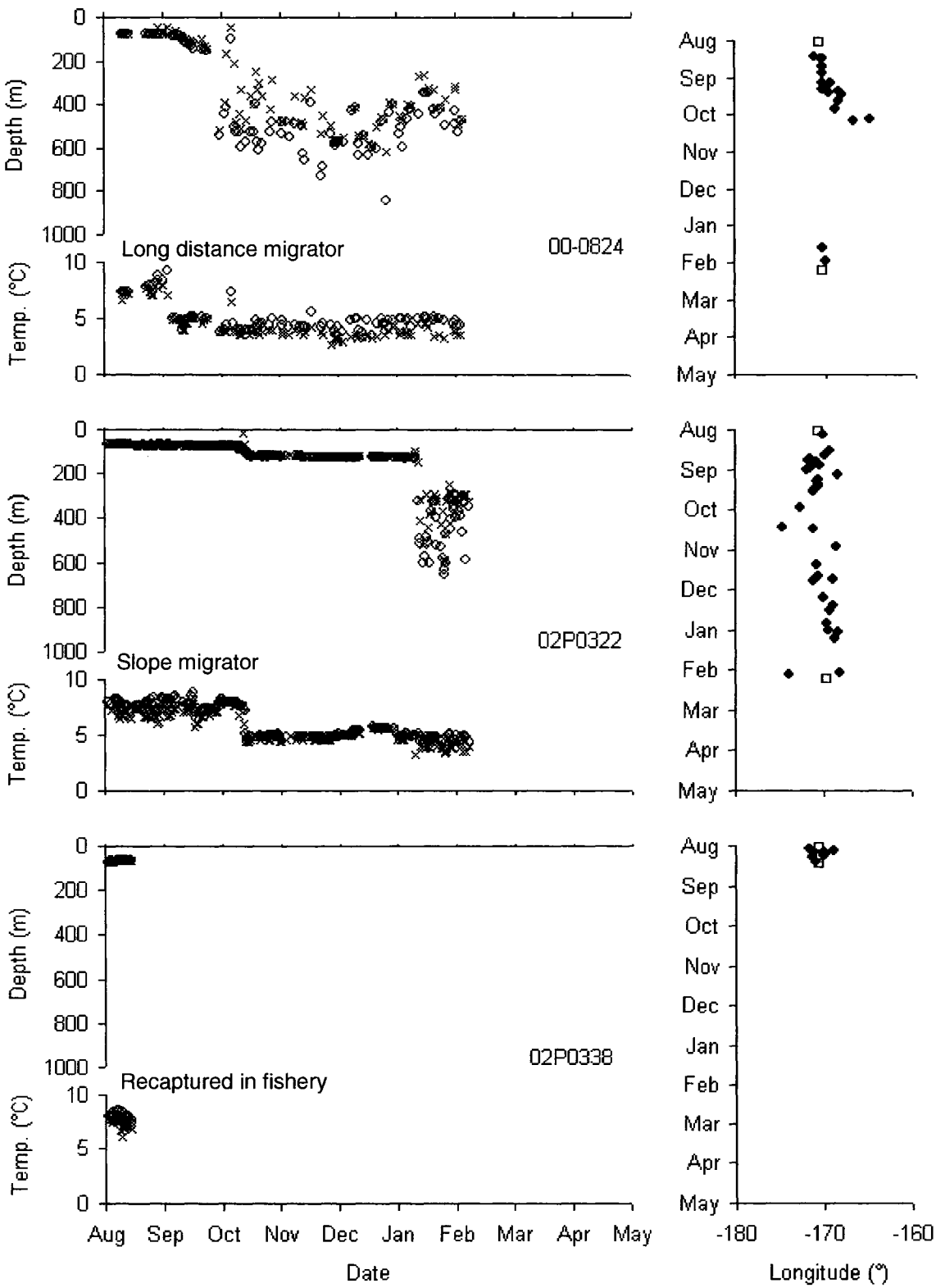


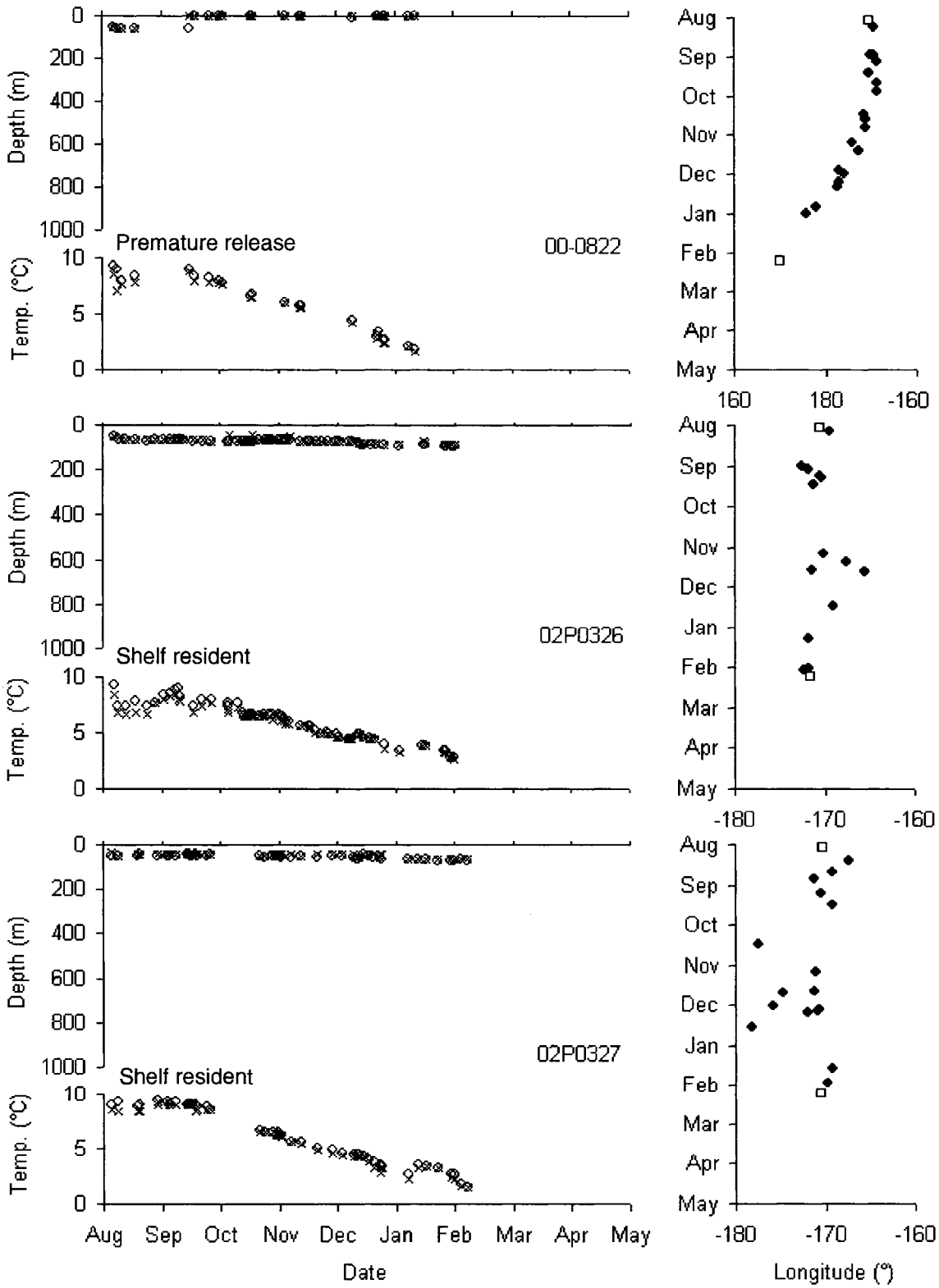


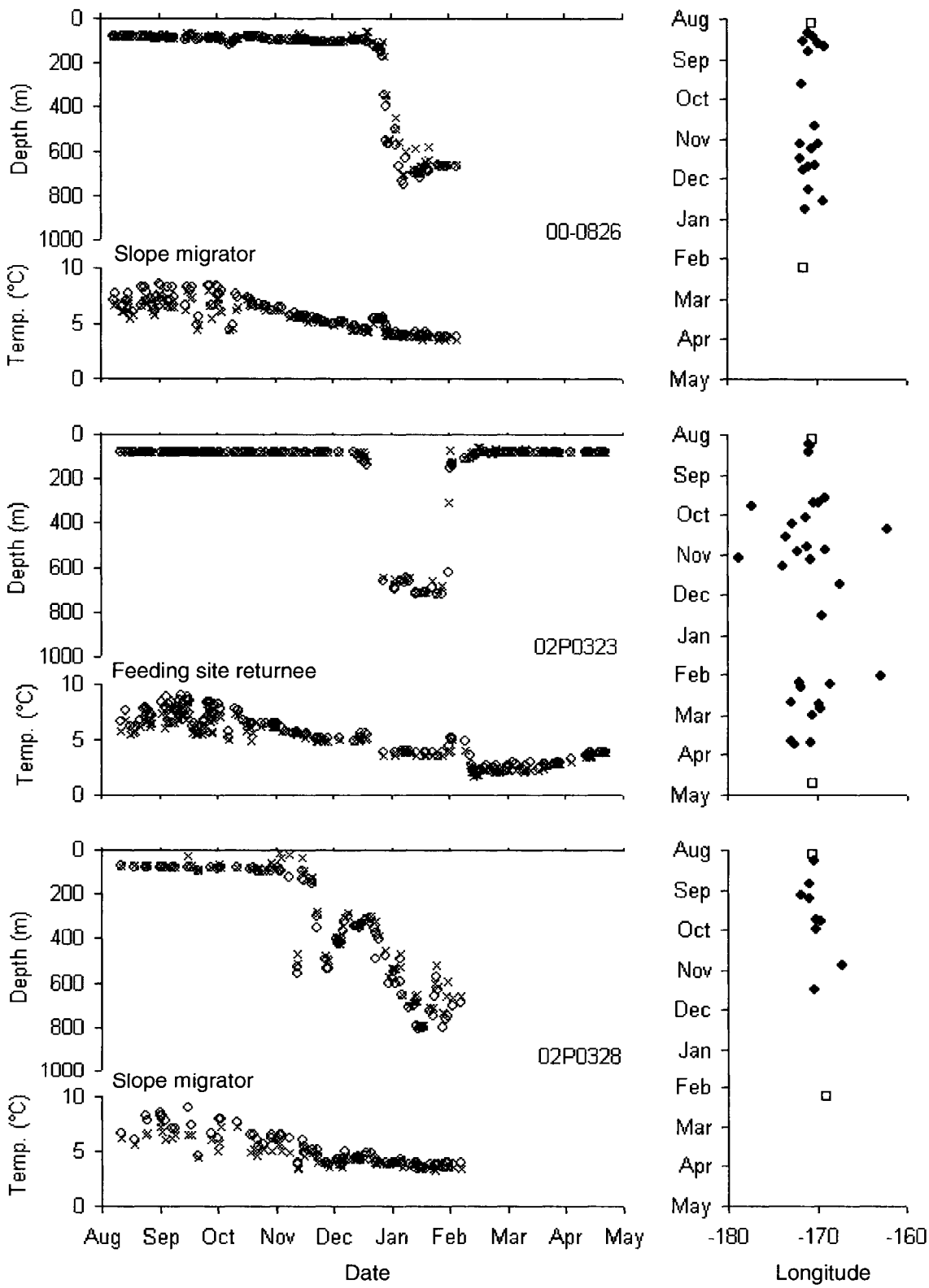
Appendix 4.4. Depth, temperature and longitude of Atka Island Pacific halibut. Maximum (o) and minimum (x) depths and temperatures are shown for each 12-hour summary period, as well as daily longitude estimates after outliers were removed. For longitude plots, □ = release position and location at which the tag reported to Argos and ● = estimated position. Tag numbers correspond to those shown in Appendix 4.3

Appendix 4.5. Deployment summary for Pacific halibut near St. Paul Island. The fish were tagged and released between 13 August and 16 August 2002, and all, but one, of the tags popped up on 15 February 2003. Tag 02P0323 popped up on 1 May 2003. Boldface print denotes tags recaptured while on the fish before the scheduled pop-off date. Tag 00-0822 prematurely released from the fish on 26 September 2002, and drifted on the surface until it reported to Argos satellites as scheduled. Because the location of the tag on the day it released from the fish is unknown, the horizontal displacement is not reported. The recovery date and days at-liberty are reported for the full duration of the tag, while the depth, temperature and geolocation data are reported for only the period in which the tag remained attached to the fish. Tag numbers correspond to those shown in Appendix 4.6. Longitude analysis is discussed fully in Seitz et al. (in press)

	00-0824	02P0322	**02P0338**	00P0822	02P0326	02P0327	00-0826	02P0323	02P0328
Fish length (cm)	124	112	112	115	127	130	114	137	119
Days at large	186	186	12	184	184	184	183	258	183
Horizontal displacement (km)	512.55	136.44	0.00	NA	73.26	16.83	101.97	5.44	129.80
Minimum depth (m)	44	16	62	52	44	40	56	56	12
Maximum depth (m)	844	652	70	64	92	72	752	724	812
Minimum temp. (°C)	2.6	3.2	6.1	7.0	2.6	1.4	3.6	1.6	3.2
Maximum temp. (°C)	9.2	8.8	8.5	9.2	9.2	9.4	8.6	9.0	9.0
Days with longitude	18	35	8	18	14	16	18	30	10
% of days with longitude	9.7	18.8	66.7	9.8	7.6	8.7	9.8	11.6	5.5
# of comparison days	0	3	8	1	2	0	1	2	1
Long. error magnitude (° ± SD)	NA	2.1 ± 1.9	0.8 ± 0.4	1.1	0.9 ± 0.3	NA	0.4	0.3 ± 0.1	0.2
Long. bias (° ± SD)	NA	0.7 ± 3.1	-0.1 ± 0.9	-1.1	-0.2 ± 1.3	NA	0.4	0.3 ± 0.1	-0.2







Appendix 4.6. Depth, temperature and longitude of St. Paul Island Pacific halibut. Maximum (o) and minimum (x) depths and temperatures are shown for each 12-hour summary period, as well as daily longitude estimates after outliers were removed. Though the same time, depth, temperature and longitude scales are used to allow comparisons among fish, data are only shown for the time period each PAT tag was at large. Tag 00-0822 prematurely released from the fish on 26 September 2002, thus subsequent recordings do not represent depths, temperatures and longitude experienced by the fish, but rather by the drifting tag. For longitude plots, □ = release position and location at which the tag reported to Argos and ● = estimated position. Note the different longitude scale for tag 00-0822 that was used because the tag prematurely released from the fish on 26 September 2002 and drifted into the eastern hemisphere. Tag numbers correspond to those shown in Appendix 4.5.

CHAPTER FIVE

Conceptual population structure of Pacific halibut (*Hippoglossus stenolepis*) using insights from satellite tagging[1]

ABSTRACT

Currently, Pacific halibut (*Hippoglossus stenolepis*) are managed as one population extending from California through the Bering Sea. However, previous satellite tagging results support the idea that the fish in the Bering Sea and Aleutian Islands belong to a separate population from those in the Gulf of Alaska. We hypothesized that separate populations may be formed by geographic and bathymetric separation, reinforced by regional behavioral adaptations to the environment. This paper compiles the results from several satellite tagging investigations of Pacific halibut and integrates the new insights into a conceptual life history model that describes mechanisms of potential population structure for Pacific halibut. Geographic landforms and discontinuities in the continental shelf appeared to limit the interchange of Pacific halibut among areas and delineated the boundaries of potential populations in the Gulf of Alaska and eastern Bering Sea, with apparent smaller, localized populations along the Aleutian Islands. The mean seasonal dispersal distance in each region appeared to be influenced by the distance between major discontinuities in the continental shelf. Regional differences in migration timing and

[1] Seitz, A.C., T. Loher, B.L. Norcross, and J.L. Nielsen. In review. Conceptual population structure of Pacific halibut (*Hippoglossus stenolepis*) using insights from satellite tagging. Fisheries Oceanography.

average monthly depth of Pacific halibut were most likely a response to different bottom temperatures and we propose that migration timing and depth evolved to maximize the survival of progeny. By using the satellite tagging results and relying on key assumptions from previous research, we built a conceptual population structure model for Pacific halibut that relied on physical and behavioral separation of spawning grounds, potential retention gyres for pelagic stages, delivery of larvae to nearshore nursery areas, and contranatant migration of juveniles.

INTRODUCTION

Pacific halibut (*Hippoglossus stenolepis*) inhabit continental shelf areas of the eastern Pacific Ocean from California to the Bering Sea. Because of their large size (up to 250 kg) and fine flesh quality, Pacific halibut have experienced sustained commercial exploitation for the last century (IPHC, 1998). Currently, this species support one of the most-profitable fisheries in the Gulf of Alaska and eastern Bering Sea. Coast-wide landings over the last five years have averaged around 70 million pounds annually, with annual landed values estimated at between US$100 and $170 million. (International Pacific Halibut Commission, unpublished).

Investigating spatial population structure, life history strategies, behavior, and habitat selection of Pacific halibut is necessary for a thorough understanding of their population biology and ecology (Best, 1981). This information is frequently needed to resolve biological questions associated with the management of the fishery, to explain

observed demographic and recruitment variation in juvenile and adult Pacific halibut and to plan research programs (St-Pierre, 1984). The International Pacific Halibut Commission (IPHC), the agency tasked with managing the Pacific halibut fishery in the Gulf of Alaska and the Bering Sea, has conducted several research programs since 1924 to investigate the biology and ecology of Pacific halibut.

One of the first and most enduring research programs has been mark-recapture studies that began in 1925 (Kaimmer, 2000). In all of the IPHC's tagging studies, conventional tags with a numeral identifier were attached to individual fish in different locations throughout their range. For each tagged fish, geoposition and biological data were recorded upon release and recapture. These investigations addressed management issues including: migration among fishing regions, rates of natural and fishing mortality, and stock identity to delineate management units (Skud, 1977; Trumble et al., 1990). Tagging results have been used to delineate management philosophy, regulations and population biology (Trumble et al., 1990).

These conventional tagging studies also have provided preliminary behavioral and ecological information. Generally, adult Pacific halibut throughout their range feed during the summer on the continental shelf, migrate to the continental slope in late fall to spawn during the winter, and in early spring migrate back to the same summer feeding grounds each year (IPHC, 1998). The spawning season occurs from early November to late March on grounds concentrated along the continental slope (St-Pierre, 1984). Winter surveys have confirmed active spawning at depths from 180 to 450 m (IPHC, 1998), while emerging data from electronic tags suggest that spawning likely occurs to depths of

800 m (Seitz et al., 2003; Loher and Seitz, 2006; Chapter 4). In addition to the continental slope, it is believed that spawning also occurs in depressions on the continental shelf (St-Pierre, 1984). After spawning, the eggs and larvae drift pelagically for six months before settling as juveniles in shallow, nearshore areas (IPHC, 1998).

Conventional tagging studies have also yielded insight into the population structure of Pacific halibut. Early experiments concluded that different segments of the population intermingle at all life stages (Skud, 1977), and therefore constitute one well-mixed population. Consequently, the IPHC manages Pacific halibut as a single population ranging from northern California through the eastern Bering Sea (see review in Chapter 4).

However, conventional tagging data are subject to several limitations. These tags only provide beginning and end positions, and growth rates if length measurements are taken at tagging and upon recovery. Conventional tagging results also are subject to biases introduced from tag shedding, mortality and differential reporting over time and area. Specifically for Pacific halibut, documentation of winter spawning locations via recovery of conventionally-tagged fish is quite rare. While tagged Pacific halibut can be legally retained by any commercial or sport fisher at any time of the year, the vast majority of tag recoveries occur via the directed fishery during the summer. From 1913 to 1924, the IPHC allowed a winter fishery on spawning grounds (Thompson and Van Cleve, 1936). At that time commercial Pacific halibut fishers were able to recover fish tagged during the summer feeding season. This allowed a brief assessment of seasonal movements from summer feeding grounds to winter spawning grounds. After 1924,

commercial fishing was closed during the winter spawning season as a protective measure, and subsequent spawning data were collected only during infrequent IPHC research cruises. The vast majority of conventional tag recoveries for Pacific halibut have been from summer feeding grounds.

Emerging technologies, such as Pop-up Archival Transmitting (PAT) tags, are able to overcome several limitations associated with conventional tagging. From October 2000 to March 2002, a pilot study in which PAT tags were attached to Pacific halibut was conducted to assess the feasibility of using these tags as a tool for identifying critical habitat of demersal fishes in high latitudes (Seitz et al., 2002; 2003). This technology successfully allowed us to gain new insights into Pacific halibut behavior and ecology, such as determining winter locations of PAT-tagged fish, inferring migration timing and depth of their seasonal migration and determining the environmental conditions experienced by the fish. Following the pilot study, we PAT tagged additional adult Pacific halibut in several locations in the Gulf of Alaska (Loher and Seitz, 2006), Bering Sea and Aleutian Islands (Chapter 4). The tags provided no evidence that Pacific halibut moved among the Gulf of Alaska, Bering Sea, and Aleutian Islands regions during the mid-winter spawning season, violating the strict assumptions of panmixis and therefore we infer that there are separate spawning populations in each region.

We hypothesize that separate Pacific halibut populations may be formed by geographic and bathymetric separation, reinforced by regional behavioral adaptations to the environment. Therefore, the goal of this paper is to integrate the new insights gained from our satellite tagging investigations into a conceptual life history model that

describes mechanisms of potential population structure for Pacific halibut. To accomplish this, we will examine regional variation in the environment and behavior of Pacific halibut and then consider how this variation may potentially form separate populations.

METHODS

For all the studies, Wildlife Computers[2] PAT tags were externally attached to Pacific halibut following a successful protocol (Seitz et al., 2003). PAT tags measured ambient water temperature, depth of the tag and ambient light. During the winter spawning season, the tags released from the fish, floated to the surface, and transmitted historical data records to the Argos satellite[3] system, during which the tags endpoint positions were determined (Keating, 1995). The Pacific halibut that were tagged were at least 105 cm fork length (FL), as they were likely to be sexually mature (Clark et al., 1999). Experiments were conducted in the Gulf of Alaska (number tagged=26; Seitz et al., 2003, Loher and Seitz, 2006), the Bering Sea (n=12; Chapter 4) and along the Aleutian Islands (n=25; Chapter 4).

The entire range of Pacific halibut was divided into three regions based upon areas among which adult Pacific halibut did not interchange in previous studies (Seitz et al., 2003, Loher and Seitz, 2006, Chapter 4): Gulf of Alaska (GOA), eastern Bering Sea (EBS), and Aleutian Islands (AI). For each region, the data from all of the fish were

[2] Redmond, Washington, USA
[3] www.argosinc.com (accessed 12 Jan. 2006)

pooled and behavioral and ecological parameters were calculated. The mean horizontal displacement by region was the average straight-line distance between the release and final locations. Only fish that were released in the summer and recovered in the winter were included in the mean horizontal displacement. The mean arrival time on the continental slope by region, which indicated arrival on the winter grounds, was the average date when the fish undertook large, abrupt, sustained changes in maximum depth while swimming from the continental shelf to the continental slope (Seitz et al., 2003). Monthly regional (i.e., GOA, EBS, and AI) depths of Pacific halibut were the average of the maximum depths from all fish in a region for each month. The depth estimate assumes that Pacific halibut spend the vast majority of their time on or near the sea floor and that maximum depths do not reflect variability in pelagic behavior (Seitz et al., 2003). Regional temperatures experienced by Pacific halibut were the mean monthly minimum and maximum temperatures from all fish in a region for each month. We chose to calculate a minimum and maximum because water temperature frequently fluctuates at a constant depth, probably with changing tidal cycles. Therefore, we did not know the proportion of time spent at specific temperatures between the minima and maxima. We did not statistically compare behavioral and ecological parameters among regions because of the low sample size of tagged fish in each region and the qualitative nature of the conceptual life history model.

Pacific halibut were classified into four behavioral types (Chapter 4): (1) Shelf residents were fish that remained on the continental shelf throughout time-at-liberty, (2) Short distance slope migrants were Pacific halibut that in winter were located on the

continental slope less than 200 km from the release site, (3) Long distance slope migrants were Pacific halibut that in winter were located on the continental slope more than 200 km from their release site, and (4) Feeding-site returnees were fish whose pop-up locations were in close proximity (<20 km) to the location at which the fish were tagged and released, but had moved to the continental slope while at-liberty.

RESULTS

Data were recovered from a total of 40 tags with 37 providing winter locations of Pacific halibut. All of the Pacific halibut tagged during the summer remained in their respective regions during the winter (Fig. 5.1). Mean horizontal displacement varied considerably among regions. The GOA fish displayed the greatest range of movement to winter grounds with an average dispersal distance of 299 ± 313.0 km (range: 7–1154 km) (Fig. 5.2) while the AI fish displayed the smallest range of dispersal to winter grounds with an average dispersal distance of 45 ± 44.9 km (range: 0.5–167 km) (Fig. 5.2). The EBS fish displayed an intermediate range of movement to winter grounds with an average dispersal distance of 162 ± 177.3 km (range: 17–512 km) (Fig. 5.2). In the GOA, long distance migrants were most common while short distance slope migrants were most common in both the EBS and AI regions (Table 5.1).

The timing of dispersal to the continental slope winter grounds also varied among regions. The fish in the GOA displayed the earliest mean arrival time on the slope with an average arrival date of 9 October ± 62 days (range: 13 July–4 January) while the EBS

fish had the latest mean arrival time with an average date of 14 December ± 41 days (range: 10 October–19 January) (Fig. 5.3). The AI fish displayed an arrival time on the winter ground intermediate to those in the GOA and the EBS with an average arrival date of 3 November ± 27 days (range: 12 September–9 December) (Fig. 5.3).

The timing of dispersal from the winter grounds back to the summer feeding grounds did not show considerable variation among regions. The dates of return to the continental shelf by the five feeding site returnees in the AI was slightly earlier (21 January ± 10 days, range: 7 January–1 February) than those in the GOA (n=2, 28 January and 16 February) and EBS (n=1, 8 February). However, these results should be interpreted with caution because of the small sample sizes.

The mean maximum depth occupied by Pacific halibut varied throughout the year and among regions (Fig. 5.4). The GOA fish displayed the smallest range in mean maximum depths by occupying the deepest water in the summer and the shallowest water in the winter. The EBS fish displayed the greatest range in mean maximum depths by occupying the shallowest water in the summer and the deepest water in the winter. The winter water depths occupied by AI fish was similar to those from the EBS, but the summer depth occupied by AI fish was intermediate to those in the GOA and the EBS.

The mean temperature range experienced by Pacific halibut varied among regions (Fig. 5.5). The GOA fish experienced temperatures that showed little intra-annual variation and remained approximately 6°C throughout the year. In contrast, the EBS fish experienced temperatures that showed considerable intra-annual variation, ranging from 8°C in the summer to 2°C in the winter. The AI fish experienced an intermediate

temperature range, with summer temperatures slightly less than the GOA, and winter temperatures slightly warmer than the EBS.

DISCUSSION

The integrated results from satellite tagging data of Pacific halibut demonstrate that potential separate populations may be formed by geographic and bathymetric separation, reinforced by regional behavioral variation in response to the environment. By combining PAT tagging data with existing oceanographic knowledge, a conceptual life history model can be built that describes potential mechanisms of population structure of Pacific halibut.

Geographic landforms and discontinuities in the continental shelf appear to limit the interchange of Pacific halibut among areas and delineate the boundaries of potential populations. The Alaska Peninsula and the Aleutian Islands form a porous barrier that in part may limit the intermingling of fish between the Gulf of Alaska and the Bering Sea. However, Pacific halibut are large, powerful swimmers that are able to disperse >1000 km seasonally (Loher and Seitz, 2006) and they easily could change regions by swimming through any of the several passes along the Aleutian Islands. Nevertheless, we have no evidence of any Pacific halibut traversing Aleutian passes in this study, including Unimak Pass, the main connection between the Gulf of Alaska and the southeastern Bering Sea. The major passes along the Aleutian Islands are discontinuities in the continental shelf with swift currents and strong turbulence (Hunt and Stabeno,

2005) that apparently deter dispersal of Pacific halibut (Chapter 4). Consequently, major passes may delineate populations of Pacific halibut. Integrating this information, our results indicate that there may be separate populations of Pacific halibut in the Gulf of Alaska and the Bering Sea divided at Unimak Pass, with smaller localized sub-populations along the Aleutian Islands.

The mean seasonal dispersal distance of individuals within these potential populations and the behavior-types of individual fish appear to be influenced by the distance between major discontinuities in the continental shelf in each region. The fish in the Gulf of Alaska demonstrated the largest mean seasonal dispersal and had the highest percentage of long distance migrants; the region also has the longest continuous continental shelf. In contrast, the fish along the Aleutian chain undertook the smallest mean seasonal dispersal and had the highest percentage of short distance slope migrants, in a region with several relatively deep passes formed by discontinuities in the continental shelf. The Aleutian Islands also had the highest percentage of feeding site returnees, which may be the result of the relatively short dispersal distance to winter grounds. Because of the short dispersal distance, the Aleutian Islands fish probably spent less time swimming to presumed spawning areas than fish from other regions and therefore the total duration of their spawning trips would be shorter, allowing the fish to arrive back on the summer grounds sooner.

We hypothesize that regional differences in seasonal dispersal, as well as timing of spawning, may have evolved to maximize the survival of their progeny by avoiding placing early life stages in relatively cold water temperatures. Comparison of the three

regions indicates that the eastern Bering Sea has the coldest continental shelf temperatures during the winter (Stabeno et al., 1999; Weingartner, 2005). Pacific halibut spawning in the Bering Sea was located in the deepest water and occurred approximately two months after that in the Gulf of Alaska. Spawning in deep areas in the Bering Sea may avoid having the juveniles develop and settle in cold winter shelf water and the eggs and larvae may not experience the cold mixed layer during their first three months of development. Rather, they probably drift at 400–700 m (Thompson and Van Cleve, 1936) in the relatively warm water of the Bering Slope Current (Kinder et al., 1975). By the time the eggs rise into the upper 200 m of the water column after almost three months of pelagic drift (Thompson and Van Cleve, 1936), the mixed layer typically starts warming (Stabeno et al., 1999). In contrast, the Gulf of Alaska has the warmest and most stable winter continental shelf temperatures of the three regions. Pacific halibut spawning in the Gulf of Alaska was located in the shallowest water and occurred approximately one month earlier than that in the Aleutian Islands and two months earlier than in the Bering Sea. The fish in the Gulf of Alaska probably were able to spawn in shallower water without exposing their eggs and larvae to the cold water found at the equivalent depths in the Bering Sea. Spawning in shallower water may be preferable to deeper water because shallower locations are closer to the inshore juvenile nursery areas which may increase the probability of successful transportation of the drifting larvae to the nursery grounds. The Pacific halibut near the Aleutian Islands, an oceanographic region formed by the combination of Gulf of Alaska and Bering Sea water masses (Ladd et al., 2005), displayed spawning characteristics intermediate to those in the Bering Sea

and the Gulf of Alaska. If the differences in regional spawning characteristics are heritable (Quinn et al., 2000; Hendry and Day, 2005), these may further reinforce separation of populations of Pacific halibut by causing spawning timing and depth segregation among populations.

An alternative hypothesis to explain regional differences in dispersal timing and average monthly depth is that adult Pacific halibut actively avoid relatively cool, shallow water during the winter, because such conditions are outside their thermal tolerance. Considering three lines of evidence from the satellite tagging data, this hypothesis seems less plausible. First, although the mean water temperature experienced by Pacific halibut in the Gulf of Alaska did not vary appreciably throughout the year and it remained in the fish's temperature tolerance range (Seitz et al., 2003), the fish still dispersed to the continental slope during the winter. Second, the shelf residents in the Bering Sea experienced water temperatures as cold as 1.4°C, which is well below previous estimates of 3°C as the minimum temperature tolerance of this species (Thompson and Van Cleve, 1936; Seitz et al., 2003). These fish could have left the continental shelf for the warmer water of the continental slope, but remained on the shelf. Third, the feeding site returnee in the Bering Sea actually left the 3.6–4.0°C water of continental slope where it spent six weeks, for the continental shelf where the water temperature remained below 3°C for the next two months. Apparently, Pacific halibut are able to tolerate relatively cold water; thus, factors other than adult temperature tolerance are probably causing the Pacific halibut to move to the continental slope.

By synthesizing the insights gained from satellite tagging with existing oceanographic knowledge, we propose a conceptual population structure model for Pacific halibut (Fig. 5.6). Spawning produces pelagic eggs and subsequent larvae that passively drift for up to seven months (Thompson and Van Cleve, 1936). During the pelagic stages, a portion of young fish may be retained in their respective regions by retention gyres (Sponaugle et al., 2002). In the Gulf of Alaska, the early life stages may be retained by meanders and eddies in the Alaska Current and the Alaska Coastal Current (Bailey and Picquelle, 2002), as well as recirculation into the Alaska Gyre (Weingartner, 2005). In the Bering Sea, the early life stages may be retained by the sluggish Bering Sea Gyre, bounded by the meandering Bering Slope Current in the east and north, the Aleutian North Slope Current in the south, and the much faster Kamchatka Current in the west (Stabeno et al., 1999). Along the Aleutians, eggs and larvae may be retained by island circulation patterns which move clockwise around continuous sections of shelf (Stabeno et al., 1999; Ladd et al., 2005) and may retain early life stages for months (Sponaugle et al., 2002). However, these gyres probably do not retain all of the larvae in their respective regions. In the Gulf of Alaska, some larvae may be carried to the Bering Sea by the Alaska Coastal Current, and some to the Aleutian Islands by the Alaska Stream. Along the Aleutians, larvae may be transported to the Bering Sea shelf by the Aleutian North Slope Current if they escape the island circulation patterns. In contrast, there is probably negligible transport from the Bering Sea to the Gulf of Alaska.

At the end of the passive larval phase, the juvenile Pacific halibut are delivered to shallow, nearshore nursery areas (Bailey and Piquelle, 2002). Several onshore transport

mechanisms may operate, including current meanders, eddies, topographic steering (Bailey and Piquelle, 2002), surface Ekman transport and the shallowing of the mixed layer that allows bottom water to move towards shore into coastal nursery areas (Weingartner, 2005). Upon arrival in nursery areas, the Pacific halibut settle as juveniles living a demersal lifestyle. During the juvenile stage, population differentiation may be maintained by contranatant migration (Cushing 1975, 1982) of the portion of Pacific halibut that were not retained in their natal regions (Skud, 1977). During the contranatant migration, juveniles that were advected among regions migrate to their natal area (Cushing 1975, 1982). Specifically for juvenile Pacific halibut, there is evidence of contranatant migration as nearly all documented movement occurs from west to east against the prevailing current (Skud, 1977). Adult Pacific halibut may not move among regions during the seasonal dispersal to winter spawning grounds, thus preventing genetic exchange at the adult life-stage between individual fish from different regions. The lack of genetic exchange by adults among regions caused by limited dispersal may be further reinforced by differences in spawning timing and depths. If this pattern is continued for several generations, separate population structure should exist in Pacific halibut.

This study has suggested potential mechanisms of population differentiation of Pacific halibut, but is also subject to limitations. The sample size of tagged Pacific halibut is small, and the behavior of the fish in each region in this study may not be truly representative of each potential population. Because of this small sample size, statistical analyses were not performed on regional parameters of Pacific halibut behavior. By increasing sample size in the future, we may be able to tag a sufficient number of fish to

represent the entire population accurately, and perform statistical analyses to determine whether the differences in regional behavior are significant. In addition to small sample size, we received less than a year of data from a fish that may live up to 50 years. These tag deployments are unable to capture observations necessary for maintaining population structure, such as regional fidelity to spawning areas and interannual dispersal. Finally, we were able to observe only a small demographic component of Pacific halibut. The fish that were tagged in this study were most likely all sexually mature females (Clark et al., 1999). Because of the large size of the tags and concern for the health of the fish, we did not attach tags to any fish smaller than 105 cm, which could be any male or immature female. To examine the movement patterns and behavior of males and immature females, we must rely on conventional tagging results until smaller satellite tags are developed.

The satellite tagging data has provided new insights for a conceptual model of how population structure may be maintained across the range of eastern Pacific halibut. Our results to date indicate that Pacific halibut populations may be formed by geographic and bathymetric separation, reinforced by regional behavioral variation in response to the environment. The results are valuable as a new starting point for generating and testing further hypotheses. In the future, we will be able to test and improve our conceptual model with additional results from satellite tagging experiments currently underway in the Gulf of Alaska and eastern Bering Sea.

ACKNOWLEDGEMENTS

This project was made possible by: Capt. H. Kalve of the F/V *Rocinante,* Capt. S. Swetzof Jr. and crew of the F/V *Wind Dancer*, Capt. R. Zwahlen and crew of the F/V *Heritage*, Capt. J. Martindale and crew of the F/V *Pacific Sun* as well as the captains and crews of the F/Vs *Angela Lynn, Bold Pursuit, Free to Wander, Norska, Pender Isle, Star Wars*, and *Waterfall* during fishing operations; International Pacific Halibut Commission (IPHC) Sea Samplers K. Attridge, B. Biffard, H. Emberton, A. Knot, E. Lardizabal, D. Rafla, J. Spencer, and A. Vatter for tagging fish; IPHC Sea Samplers R. Ames, E. Ekroth, L. Mattes and A. Williams, and D. Wilson of United States Geological Survey-Alaska Science Center for tagging assistance to the senior author; IPHC Port Sampler L. O'Neil for St. Paul Island logistics; IPHC Annual Setline Survey Managers C. Dykstra and K. Ames for logistical assistance; P. Lestenkof of Central Bering Sea Fishermen's Association for housing on St. Paul Island. Partial funding for this project was provided by the Exxon Valdez Oil Spill Trustee Council, the International Pacific Halibut Commission, the U.S. Geological Survey–Alaska Science Center and the University of Alaska Fairbanks School of Fisheries and Ocean Sciences. The findings presented by the authors are their own and not necessarily the position of the EVOS Trustee Council.

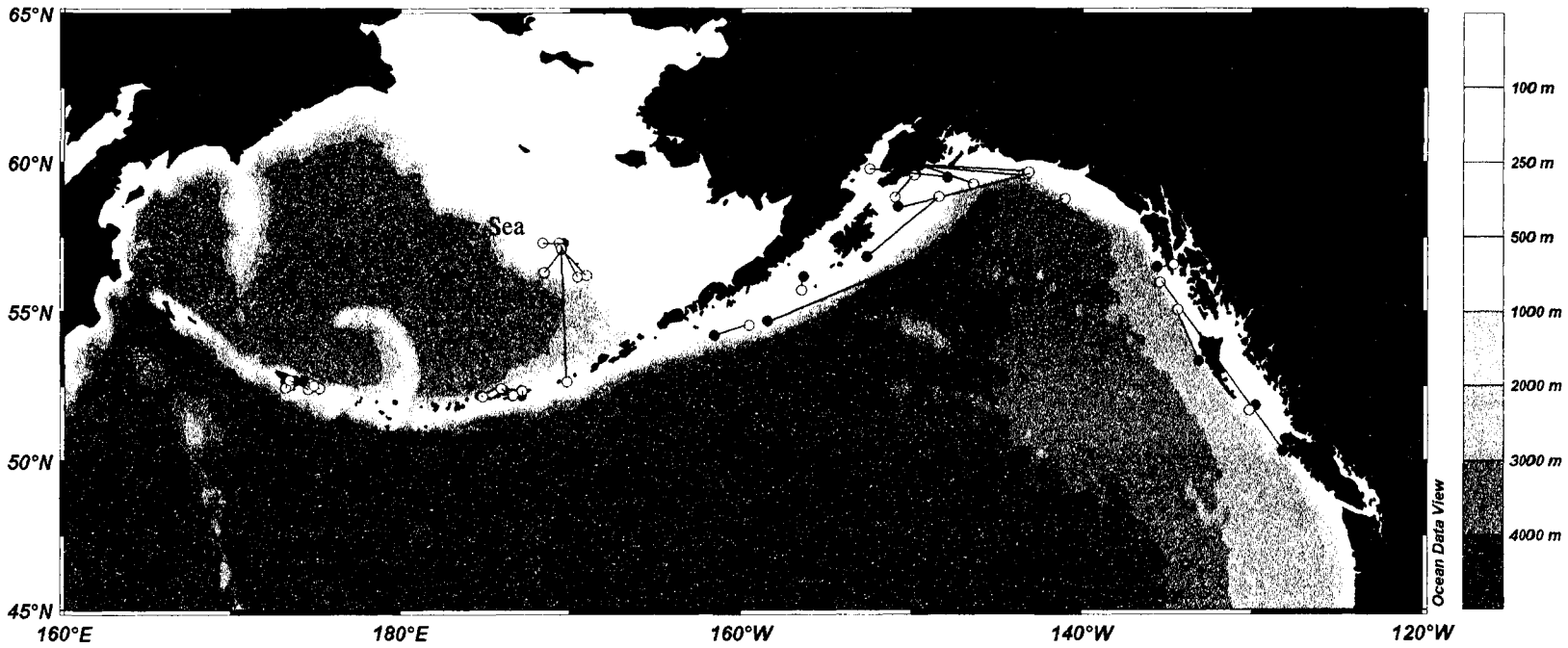


Figure 5.1. Release (●) and winter recovery sites (o) of PAT-tagged halibut in the North Pacific Ocean

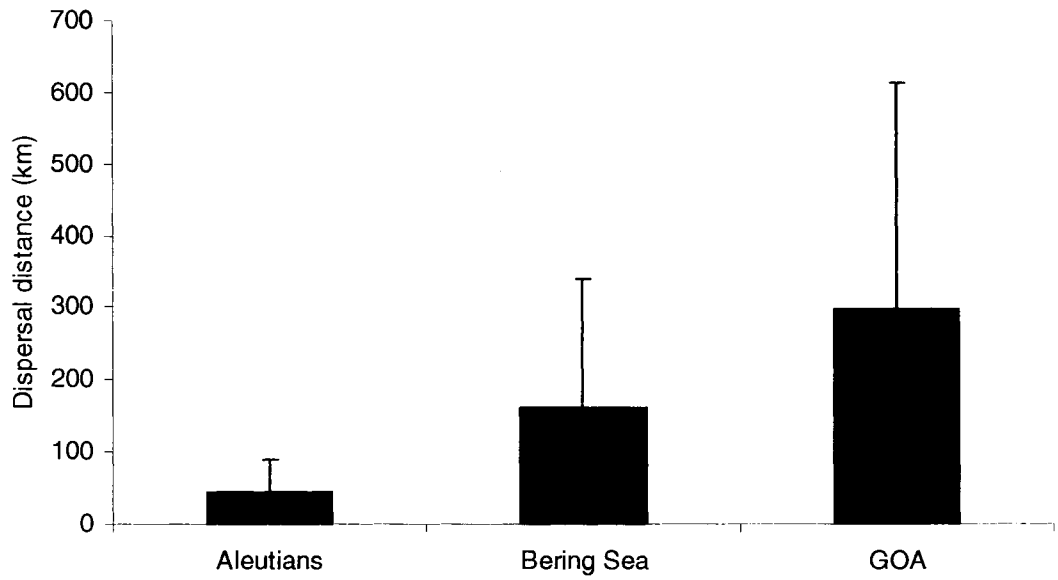


Figure 5.2. Average seasonal dispersal distance of Pacific halibut in three regions. Dispersal distances were calculated as the straight-line distance between the release and recovery sites.

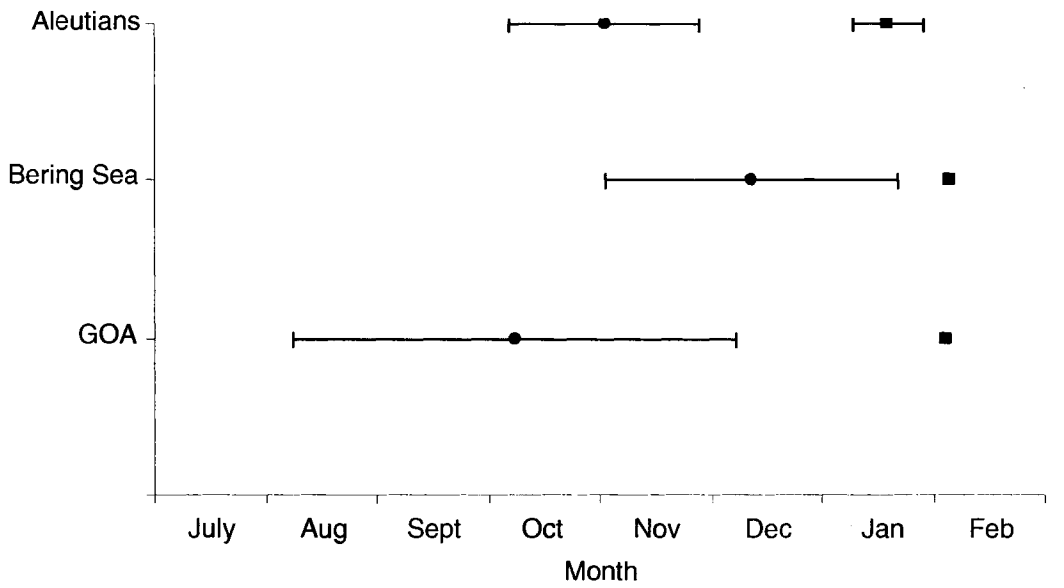


Figure 5.3. Mean arrival dates (●) by region of Pacific halibut at the continental slope, which serve as a proxy of arrival on spawning grounds. Arrival on the slope was defined as the first time that the fish exceeded depths of 200 m. Mean departure dates (■) from the continental slope, which serve as a proxy of returning to summer feeding grounds. Error bars are not shown for the Bering Sea and the Aleutian Islands because the departure date was calculated from one and two fish respectively.

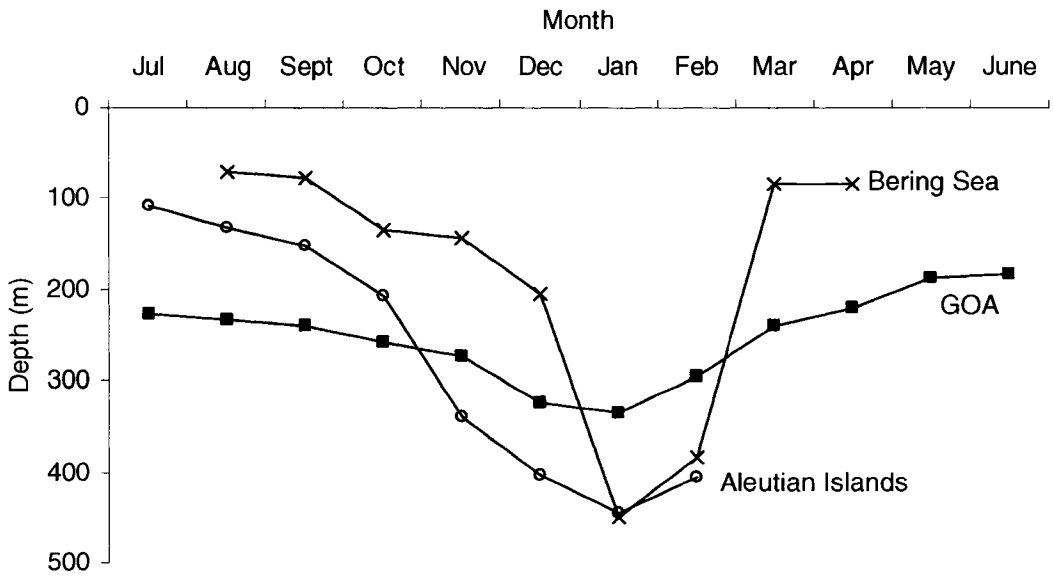


Figure 5.4. Monthly mean maximum depth of Pacific halibut in three regions. Error bars are not shown because they overlapped substantially making interpretation difficult. GOA=Gulf of Alaska.

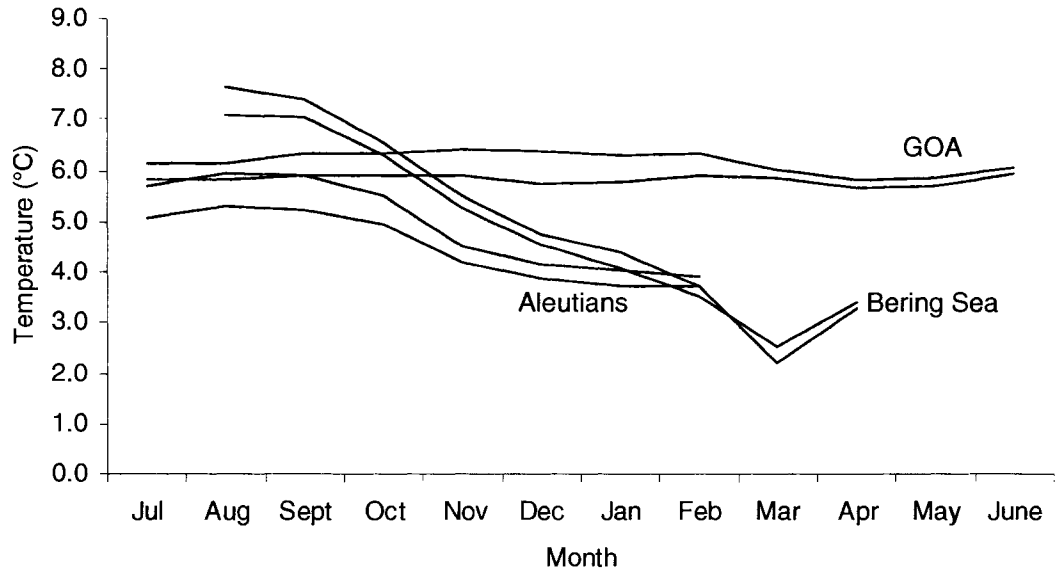


Figure 5.5. Monthly mean minimum and maximum temperatures experienced by Pacific halibut in three regions. Error bars are not shown because they overlapped substantially making interpretation difficult. GOA=Gulf of Alaska

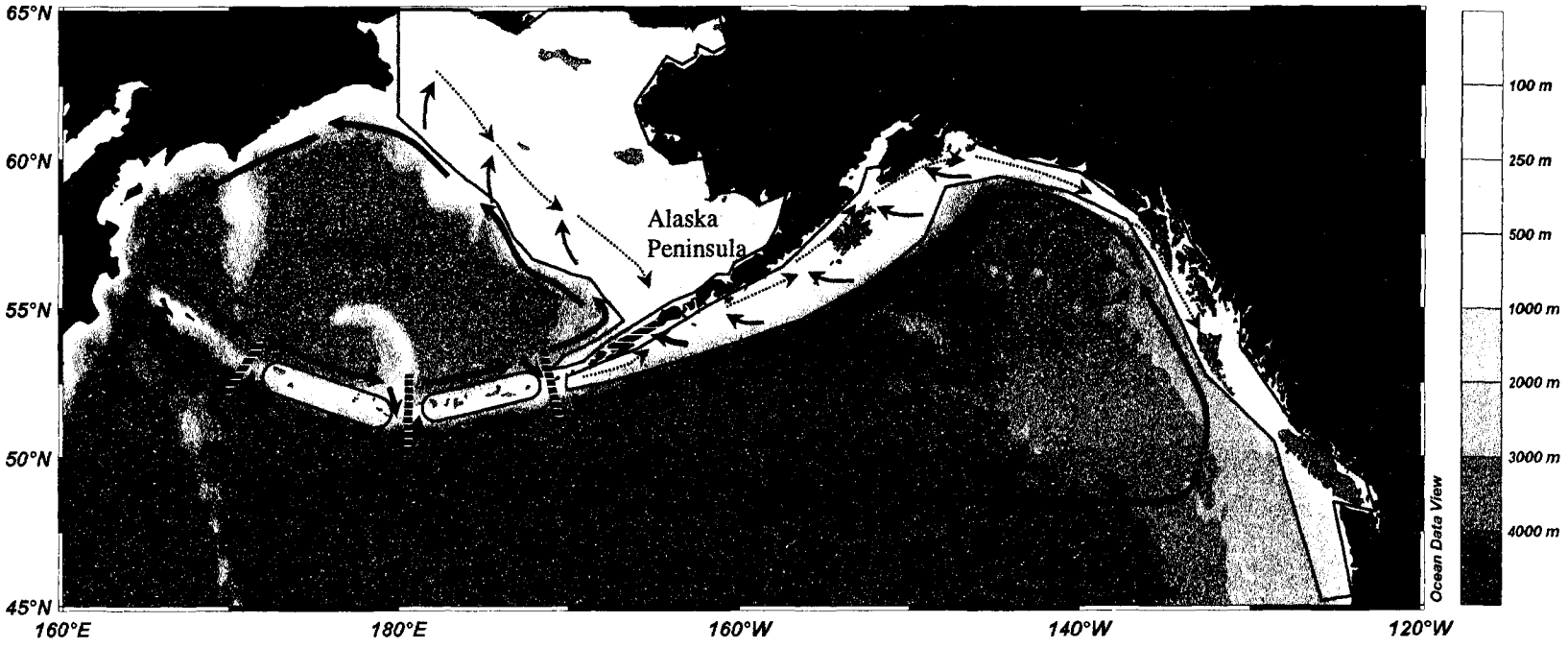


Figure 5.6. Conceptual populations of Pacific halibut and the mechanisms that may produce them. Transparent gray areas indicate potential populations. Thick solid arrows indicate predominant currents. Thin solid arrows indicate semi-permanent current features such as retention eddies, meanders and onshore transport. Thin dashed arrows indicate contranatant migration by juveniles. Thick lines with white stripes indicate areas of limited adult movement

Table 5.1. Behavior types of Pacific halibut in three regions. * indicates tags that were recovered during the summer feeding season, rather than during the winter spawning season.

	Shelf resident	Short distance slope migrant	Long distance slope migrant	Feeding site returnee
GoA	4	3	8	2*
Bering Sea	2	3	1	1*
Aleutians	2	9	-	5

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Conclusions

This study has provided a major advance in our knowledge of Pacific halibut biology and ecology. Using Pop-up Archival Transmitting (PAT) tags I was successfully able to determine winter locations of Pacific halibut, to infer migration timing and depth of seasonal migration, and to determine the environmental conditions experienced by the fish. In Chapter 2, geolocation by ambient light was able to discern basin-scale movements of demersal fishes in high latitudes and therefore this technique provided a feasible method for providing scientific inference on large-scale population structure in Pacific halibut. Because seasonally low ambient light levels and inhabitation of deep water (>200 m) restricted geolocation by light during winter, a minimum-distance dispersal model was developed for identifying migration pathways of demersal fish in the Gulf of Alaska based on daily maximum depth (Chapter 3).

Using the techniques developed in the previous two chapters, the PAT tags provided no evidence that Pacific halibut in the southeastern Bering Sea and Aleutian Islands dispersed to the Gulf of Alaska during the mid-winter spawning season, supporting the hypothesis that there are separate spawning populations in the Gulf of Alaska and Bering Sea/Aleutian Islands (Chapter 4). In Chapter 5, I proposed a conceptual population structure model in which geographic landforms and discontinuities in the continental shelf appeared to limit the interchange of adult Pacific halibut among regions and possibly delineate the boundaries of potential populations of Pacific halibut in the Gulf of Alaska and eastern Bering Sea, with apparent smaller, localized populations along the Aleutian Islands. Regional variation in spawning timing and depth

in response to the thermal environment of each region may reinforce separation of populations (Quinn et al. 2000). Each of these three regions has a potential retention area for eggs and larvae (Stabeno et al. 1999), which may maintain the potential population structure established by the limited exchange among regions by adults.

The study was subject to several limitations that should be used to direct future research. Additional PAT tags are needed to increase the sample size of tagged Pacific halibut in the Gulf of Alaska, Bering Sea and Aleutian Islands. The exact number of tags that is needed in each region is currently inestimable (D. Johnson, National Marine Fisheries Service, Seattle, WA, personal communication) because insufficient baseline data exist to design a quantitative experiment *a priori*. To design a Pacific halibut tagging experiment quantitatively, one would have to conduct a sample size estimation and power analysis. To conduct a power analysis for detecting Pacific halibut population delineation, a statistical test must first be specified. Next, true population values that are being tested, such as dispersal and seasonal locations, must be specified. However, true population values of dispersal and seasonal locations are not known because insufficient baseline data exist. To address this problem, the sample size of PAT tags attached to Pacific halibut that release during the winter spawning season was increased during the summer of 2006 when 24 and 78 PAT tags were deployed in the Bering Sea and the southern Gulf of Alaska (T. Loher, International Pacific Halibut Commission, Seattle, WA, personal communication). These deployments will add to the baseline data in these regions, but additional Pacific halibut in the Aleutian Islands and northern Gulf of Alaska should be PAT tagged.

To quantitatively test for separate populations of Pacific halibut in the Gulf of Alaska, Bering Sea and Aleutian Islands, cluster analysis should be conducted on the dispersal data of adult fish (D. Johnson, National Marine Fisheries Service, Seattle, WA, personal communication). In the case of Pacific halibut, the seasonal locations may be grouped into regional clusters (Everitt et al. 2001). Cluster analysis of movement has been used successfully to delineate polar bear (*Ursus maritimus*) populations in Greenland and Canada (Taylor et al. 2001). Similar to Pacific halibut, the polar bear populations were delineated by physiographic features that caused discontinuities in their movements. The results of the polar bear cluster analysis agreed closely with other techniques such as genetic information, mark-recapture data and traditional knowledge of Inuit hunters. Therefore, cluster analysis can potentially identify populations of free-ranging animals and should be considered for Pacific halibut.

Monitoring of other demographic components of the Pacific halibut population is needed. The fish that were tagged in this study were most likely all sexually mature females (Clark et al. 1999). Because of the large size of the tags and concern for the health of the fish, tags were not attached to any fish smaller than 105 cm, which could be any male or immature female. Most of the knowledge about the dispersal and seasonal locations of small Pacific halibut (<105 cm) comes from conventional tagging experiments, which are subject to several limitations and their conclusions are questionable (Chapter 4)

Alternative technology such as archival tags or acoustic tags will allow examination of the dispersal, seasonal locations and behavior of males and immature

females. Archival tags contain the same sensors as PAT tags, but do not contain a release mechanism; therefore they are dependent on fish recapture for data recovery (Arnold and Dewar 2001). Geolocating archival tags are approximately 60% smaller than PAT tags and could be attached to the smallest Pacific halibut, 45 cm, captured on longline fishing gear. Archival tagging experiments are currently underway on captive Pacific halibut in aquaria to test the feasibility of tagging fish that are not large enough to carry PAT tags (T. Loher, International Pacific Halibut Commission, Seattle, WA, personal communication). If archival tags are feasible for studying small Pacific halibut (<105 cm), fish should be tagged and released in the Gulf of Alaska, Bering Sea, and Aleutian Islands to study their dispersal, seasonal locations and behavior.

Another alternative technique, acoustic tags, may be used on fish as small as 12 cm (Welch 2005). These tags repeatedly emit a unique identification code, which is detected and recorded by receivers on the seabed whenever a tagged fish comes within a receiver's listening range (Arnold and Dewar 2001). There are long-range plans for the Pacific Ocean Shelf Tracking project[1] that involve the deployment of 30 or more monitoring lines of acoustic receivers on the seabed of the continental shelf from California to the Gulf of Alaska (Welch 2005). If small Pacific halibut were tagged with acoustic tags, the dispersal of individual fish can be reconstructed using the time of detection on different monitoring lines.

Alternative methodologies to PAT tags are needed to examine potential separate populations of Pacific halibut in the Gulf of Alaska, Bering Sea and Aleutian Islands on

[1] www.postcoml.org <accessed 15 August 2006>

interannual, lifetime and intergenerational timescales. The PAT tag deployments in this study provided less than a year of data from a fish that may live up to 50 years. These tag deployments are unable to capture observations necessary for maintaining population structure, such as regional fidelity to spawning areas and interannual dispersal. Longer deployments of PAT tags are not recommended because of premature release of the tags caused by stress on the tether assembly (Arnold and Dewar 2001).

For interannual timescales, archival tags can provide fine scale behavioral information as these tags are able to store up to 4.5 years of data when sampled every minute and battery life exceeds the memory capacity of the tag. Archival tags have successfully confirmed migration route and spawning site fidelity in successive spawning seasons in European plaice (*Pleuronectes platessa*) (Hunter et al. 2003) and could be used to answer the same questions about Pacific halibut. The battery life of acoustic tags may provide up to 20 years of movement data if a Pacific halibut swims past acoustic receivers during its time at-liberty.

For lifetime scales, the study of otolith chemistry, in which the chemical signature of the fish's earbone is matched with the unique chemical signature of different areas of the ocean, should enable assignment of nursery areas for individual fish (Thorrold et al. 2001), as well as the areas occupied during different stages of a fish's life (Kennedy et al. 2002). Using otolith chemistry, movement among regions can be examined for individual fish. Otolith chemistry of Pacific halibut from select locations in the Gulf of Alaska and southeast Bering Sea is being examined to test the feasibility of assigning nursery origin of adult Pacific halibut and the movement of juveniles (Loher and

Wischniowski 2006). If otolith chemistry proves feasible for assigning nursery areas and studying juvenile movement, this technique should be used to study Pacific halibut throughout their range in the Gulf of Alaska, Bering Sea and Aleutian Islands.

For intergenerational timescales, genetic techniques may be used to examine possible population differentiation in different regions of the range of Pacific halibut. Two independent genetic analyses are currently being conducted on Pacific halibut from select locations in the Aleutian Islands, Bering Sea and Gulf of Alaska to optimize genetic markers and determine whether significant genetic differences occur among fish from each region (J. Nielsen, United States Geological Survey-Alaska Science Center, Anchorage, AK, personal communication; Hauser et al. in press). Once genetic markers are optimized, both male and female Pacific halibut from several year classes should be sampled in the Gulf of Alaska, Bering Sea and Aleutian Islands to test for genetic difference among sexes, year classes and regions.

The timing of tagging and sampling needs to be considered for discerning population structure in Pacific halibut. Tagging and sampling are accomplished most easily during the International Pacific Halibut Commission Summer Setline Survey (Dykstra et al. 2006). In this survey, a regular grid of stations in the Gulf of Alaska, eastern Bering Sea and Aleutian Islands is fished annually during the summer for stock assessment purposes. Ancillary projects are readily accommodated during the survey; hence most Pacific halibut research is conducted during the summer. However, Pacific halibut are on their feeding grounds during the summer and are not spawning, therefore genetic mixing does not occur during this time. A concerted effort needs to be made to

tag Pacific halibut and collect biological samples during the winter on the spawning grounds where the actual genetic exchange among individuals occurs. It is during this time that actual population components are defined.

Given the economic importance of Pacific halibut in the North Pacific Ocean, accurate description of their population structure is paramount to a sound management plan. If Pacific halibut in the Gulf of Alaska, Bering Sea and the Aleutians Islands belong to different populations, it would be biologically appropriate to divide the entire range of Pacific halibut into smaller sub-units with independent population dynamics, catch quotas and/or exploitations rates. Each region could be managed independently essentially producing local area management plans that more accurately reflect population structure.

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